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Frogs of the *Eleutherodactylus biporcatus* Group (Leptodactylidae) of Central America and Northern South America, Including Rediscovered, Resurrected, and New Taxa

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CONTENTS

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ABSTRACT

A revision of the broad-headed frogs of the *biporcatus* species group of *Eleutherodactylus* s.l. has a wholly unexpected nomenclatural consequence. *Eleutherodactylus biporcatus* (W. Peters, 1863) is not from "Veragua" (western Panama) as originally thought, but is the proper name for the Venezuelan frog heretofore known as *E. maussi* (Boettger, 1893).

Three names are resurrected from synonymy for Central American species currently masquerading under the misapplied name *biporcatus*, and a fourth species is described as new: (1) The rediscovery of *Eleutherodactylus gulosus* (Cope, 1875) shows it to be a large montane frog occupying an apparently small range in the borderland of Costa Rica and Panama. (2) *Eleutherodactylus rugosus* (W. Peters, 1863) is a smaller species occurring on the Pacific versant of southwestern Costa Rica and western Panama; *Lithodytes pelviculus* Cope and *L. florulentus* Cope are synonyms of *E. rugosus*. (3) *Eleutherodactylus megacephalus* (Cope, 1875), an intermediate-sized frog ranging from Honduras to central Panama, is the more common species to which the name *biporcatus* has usually been applied. Available material from the western half of the Isthmus of Panama was too sparse to decide if another (unnamed) species is being included under the name *megacephalus*. (4) The name *biporcatus* also has been used for *Eleutherodactylus opimus*, new species, which occurs from central Panama to western Colombia.

Based on the condition of the m. adductor mandibulae, the Venezuelan *Eleutherodactylus biporcatus* s.s. (*E. maussi*, auctorum) belongs to the Middle American clade of *Eleutherodactylus* (subgenus *Craugaster*). However, preliminary data on karyotypes, as well as morphological differences, cast doubt on the closeness of *E. biporcatus* to the other species studied. The monophyly of the "*biporcatus* group" therefore remains to be tested.

RESUMEN

La revisión de las ranas de cabeza ancha del grupo *biporcatus* de *Eleutherodactylus* tiene una consecuencia nomenclatural completamente inesperada. *Eleutherodactylus biporcatus* (W. Peters, 1863) no es de "Veragua" (Panamá occidental) como se creía previamente, sino que es el nombre propio de la rana venezolana conocida hasta ahora como *E. maussi* (Boettger, 1893).

Se resucitan tres nombres de la sinonimia para especies centroamericanas previamente ocultos bajo el nombre incorrecto de *biporcatus*, y se describe una cuarta especie nueva: (1) El redescubrimiento de *Eleutherodactylus gulosus* (Cope, 1875) indica que es una rana grande, de montaña, que tiene una distribución geográfica pequeña en la frontera entre Costa Rica y Panamá. (2) *Eleutherodactylus rugosus* (W. Peters, 1863) es una especie más pequeña que ocurre en las tierras más bajas del Pacífico del suroccidente de Costa Rica y del occidente de Panamá; *Lithodytes pelviculus* Cope y *L. florulentus* Cope son sinónimos de *E. rugosus*. (3) *Eleutherodactylus megacephalus* (Cope, 1875), una rana de tamaño intermedio y distribuida desde Honduras hasta Panamá central, es la especie que más comunmente se ha llamado *biporcatus*. El material disponible de la mitad occidental del Istmo de Panamá no es adecuado para decidir si hay alguna otra especie (sin nombre) incluida bajo el nombre *megacephalus*. (4) El nombre *biporcatus* también se ha usado para *Eleutherodactylus opimus*, especie nueva, que ocurre desde Panamá central hasta Colombia occidental.

Basándose en la condición del m. adductor mandibulae, *Eleutherodactylus biporcatus* s.s. (*E. maussi* auctorum) de Venezuela pertenece al clado mesoamericano de *Eleutherodactylus* (subgenero *Craugaster*). Sin embargo, información preliminar sobre cariotipos, así como diferencias morfológicas, hacer dudar del parentesco de *E. biporcatus* con las otras especies estudiadas. La monofilia del "grupo *biporcatus*" debe ser corroborada.

INTRODUCTION

In the lowlands and on the adjacent slopes of lower Central America, some of the most commonly seen leaf-litter anurans are small, broad-headed, diurnal, toadlike *Eleutherodactylus* that usually have large white ventral spots in a dark reticulum. On the Atlantic side of Costa Rica, the little frogs are further characterized by a coloring of red or orange on the posterior venter and undersides of the hands and feet. These frogs have been referred to as *Eleutherodactylus biporcatus* by most recent authors following Dunn (1931).

However, the impressions gained of these animals based on diurnal observations of the small juveniles are illusionary, for the adults are large (to 70 mm SVL), seldom-seen nocturnal predators. They may typically hide in burrows during the day, and come to the surface at night to ambush passing prey, including large arthropods and even small frogs and lizards.

Unlike most species in this huge genus of over 500 species, males seemingly do not vocalize.[3] As a result, adult males, which are usually located by their sounds in other species, are underrepresented in collections; at well-sampled sites, females are obviously disproportionately represented among adults. Reproductive behavior is unknown, but eggs are probably laid in the leaf litter where the juveniles abound.

The present study has developed from two different lines of research, each questioning the allocation of all lower Central American specimens of these broad-headed frogs to a single species. Savage has had a longtime commitment to elucidating the composition of, and relationships within the genus *Eleutherodactylus*, especially in Central America. For some time he had thought that more than one species was subsumed under the name *Eleutherodactylus biporcatus*, but believed that a review of broad-headed frogs nominally of that taxon from throughout its range was necessary to confirm or reject this hypothesis. Myers was particularly interested in the genus in the context of its species and their distribution on the Panamanian Isthmus. His own fieldwork in western Panama had led him also to conclude that more than one species probably was represented by the monolithic *E. biporcatus*. In the process of beginning to resolve this problem, Myers was able to borrow several critical type specimens from the Berlin Museum, through the courtesy of Dr. Rainer Günther.

Serendipitously, the two lines of research converged on the occasion of the 62nd annual meeting of the American Society of Ichthyologists and Herpetologists at the American Museum of Natural History, in June 1991, when conjoint examination of the Berlin type material convinced us of the need for this collaborative analysis. In its course, we examined extensive series of *biporcatus*-like frogs, the type specimens of all nominal Central American taxa thought to be synonyms of *E. biporcatus*, and the types of valid related species. Our primary goal in the study is to determine the systematic status, distribution, and relationships of *E. biporcatus* and its allies and to establish a proper nomenclature for included valid taxa.

Our manner of presentation of the results of study departs somewhat from traditional systematic papers where an a posteriori logical framework is imposed on the not necessarily logical sequence of investigation. Rather, as in the genre of detective fiction, we have tried for the most part to present each clue leading to our conclusions in the order of discovery. As in such tales, there were several real surprises and a few false leads as well.

Methods

Description of the external morphology of the included taxa follows, where appropriate, the characters defined in Lynch and Duellman (1980, 1997) and Savage (1975, 1987). The presence or absence of paired dorsal ridges (plicae) is important in the taxonomy of this group. For convenience, we use the term *suprascapular plicae* for the anterior ridges, even though they may extend posteriorly from the eyes to midbody in some species. One species has *paravertebral plicae* positioned at midbody, separate from the suprascapular plicae. The posterior or *laterosacral plicae,* when present, are often less well defined, sometimes comprising only slightly raised, linear rows of small tubercles.

Measurements were taken with a dial caliper to 0.01 mm and rounded to the nearest 0.1 mm. Head-body length is indicated by the abbreviation SVL, which may be read ei-

[3] This is an inference based on never having seen one calling. The males of all but one species in the group do lack vocal slits (hence vocal sacs), but absence of these structures is not a reliable predictor of voicelessness. Vocal sacs have been lost in diverse species of frogs that, however, retain well-developed advertisement calls (e.g., Myers, 1982: 4–5 [*Dendrobates reticulatus*]; Zweifel, 2000: 72–73 [*Liophryne similis*]). And voice in female frogs does not depend on such structures (see Natural History in systematic section, under *Eleutherodactylus biporcatus*).

ther as snout-vent length or amphibian standard length (distance from the tip of the snout to posterior margin of vent); for these frogs there is no practical difference between the definitions, inasmuch as the vent opens in a vertical plane. Measurements, taken mostly by the first author over a period of time, involve specimens both poorly and well preserved. For this reason and, especially, because significant population samples of adults are nearly lacking, we provide only simple quantitative values without statistical analyses.

The color descriptions emphasize colors in life, which are based on our field notes and color slides. In the Systematic Synopsis these summarize variation in the most obvious and/or distinguishing features. Most bright colors, especially reds, yellows, and greens are lost more or less rapidly on preservation, while darker ones tend to be intensified. Consequently the general pattern, uniform, spotted blotched, striped, etc., is similar in life and preservation. Other aspects of coloration and pattern markedly affected by preservation beside those just mentioned are indicated where appropriate.

Taxonomic History

The frogs of the genus *Eleutherodactylus* Duméril and Bibron, 1841 were referred to various genera during the 19th and early 20th century (G. Myers, 1962). Original species descriptions and subsequent references to the taxa discussed below used the names *Hylodes* Fitzinger, 1843, *Lithodytes* Fitzinger, 1843, and *Strabomantis* W. Peters, 1863, until (and even after) Stejneger (1904) concluded that most species in the nominal *Hylodes* and *Lithodytes* should be placed in *Eleutherodactylus*. Many workers of this period applied the name *Hylodes* to all these frogs, but Cope (1862: 153–154) divided that genus into several groups, including *Hylodes*, with typically granular venters, and *Lithodytes*, with smooth venters, a distinction no longer recognized.

In 1863, Wilhelm Peters erected a new genus and species for a broad-headed frog from "Veragua" that he called *Strabomantis biporcatus*. Veragua was the name of a Province of New Granada and used at that time for much of what is now western Panama, including today's provinces of Bocas del Toro, Chiriquí, and Veraguas. Interestingly, in the same paper he described an unrelated *Eleutherodactylus* as *Hylodes gollmeri*, based on two frogs purportedly from Caracas, Venezuela (lectotype ZMB 3168, paralectotype ZMB 36301; originally identified by Lichtenstein and von Martens [1856] as *Hylodes martinicensis* from "Cavacas").

Subsequent study (Rivero, 1961; Savage, 1987) suggested that an inadvertent exchange of data may have occurred between the aforesaid type specimens of *Hylodes gollmeri* and some types of *Phrynidium* (= *Atelopus*) *crucigerum* Lichtenstein and von Martens (1856). Although a few extant "types" of *Phrynidium crucigerum* are from the published type locality "Veragoa", others are conspecific with a species (usually called *Atelopus cruciger*) inhabiting the Cordillera de la Costa of Venezuela.[4] On the same hand, the types of *Hylodes gollmeri* are representatives of a rather common but distinct Panamanian species of *Eleutherodactylus*. A

[4] In a recent paper, Lötters et al. (1998) confirmed that specimens labeled (in ZMB) as syntypes of the name *crucigerum* are from both Panama and Venezuela. They however selected a nonlabeled specimen (ZMB 3380) from "Veragoa" (western Panama) as the lectotype and synonymized *Phrynidium crucigerum* with the Central American *Atelopus varius*. Lötters et al. proposed a scenario whereby ZMB 3380—a single specimen which has "no indication of type status" collected by J. Warszewicz—must have been cataloged with at least four other specimens that may subsequently have been lost or exchanged (*crucigerum* supposedly was based on five specimens from Veragoa).

They asserted that Venezuelan specimens could not have been used for the original description because of a difference in skin texture. However, as is well known, early authors commonly based descriptions on single specimens drawn from whatever sample of "cotypes" (syntypes) was at hand.

Considering the poor original description and all the assumptions made by Lötters et al. as to what is or might have been one of the original types, they might have better served stability by designating a syntype that was cataloged as such and that would have preserved the well-known name *Atelopus cruciger* for the Venezuelan frog. The matter would now seem nomenclaturally disposed of, except for the arguable question as to whether the "lectotype" was indeed part of the syntype series as postulated by Lötters et al.

similar error in locality data associated with old Berlin Museum type specimens will be shown later in this paper to have serious implications for the provenance and identity of *Strabomantis biporcatus*.

Peters (1873) later described a second broad-headed form as *Hylodes rugosus* from "Chiriqui" without reference to his earlier-named *Strabomantis biporcatus* from Veragua. The name Chiriquí was used at that time for western Veragua Province and is essentially equivalent to today's Panamanian provinces of Bocas del Toro and Chiriquí.

Shortly thereafter, Cope (1875) recognized two additional broad-headed taxa, *Lithodytes megacephalus* and *Lithodytes gulosus*, collected on W. M. Gabb's expedition to the southern Cordillera de Talamanca of Costa Rica. A few years later Cope (1877: 89) described *Lithodytes pelviculus*, "said to have been found on the west coast of Central America". Boulenger (1882: 198–220) and Brocchi (1882: 49–59) simultaneously placed *Strabomantis* in the synonymy of *Hylodes*, in which they recognized all five of the broad-headed species mentioned above. Cope later (1893: 336) maintained *Lithodytes* for the three species that he had named (*gulosus*, *pelviculus*, *megacephalus*) and described another (*Lithodytes florulentus*) from Boruca in the Pacific drainage of southwestern Costa Rica.

Günther (1900–1901 [1885–1902]) treated *biporcatus* (p. 231), *rugosus* (p. 233), *florulentus* (p. 234), *megacephalus* (p. 239), and *gulosus* (p. 240) as distinct taxa of *Hylodes*. Günther (op. cit.) also had intended to treat *Lithodytes pelviculus* as a valid species of *Hylodes*, as shown by its inclusion as species no. 23 in his key on page 227 (where it is misspelled "*petriculus*" [fide erratum on p. xx]), but subsequently changed his mind and allocated the name to the synonymy of *H. megacephalus* (p. 239).

Nieden (1923: 432–439, 466) followed Günther's (1901) assignments for the Central American species, and also picked up the name *Hylodes maussi* Boettger (1893) for a South American broad-headed species apparently related to this complex, from Puerto Cabello, on the Caribbean coast of Venezuela.[5]

Noble (1918: 329–331) used the name *Eleutherodactylus rugosus* for examples of this group from Nicaragua and placed *Lithodytes megacephalus* and *L. pelviculus* in its synonymy. He concluded that his "large series of specimens shows conclusively that *E. megacephalus* is but the adult of *E. rugosus*". Noble retained *L. gulosus* as a valid species of *Eleutherodactylus* similar to but larger than *megacephalus/rugosus*.

Stejneger (1904) had revived usage of the name *Eleutherodactylus* for frogs placed in the *Hylodes* and *Lithodytes* of previous authors, a course followed by most subsequent workers. Dunn (1931) used the name *Eleutherodactylus biporcatus* for the Panamanian species and, according to his unpublished notes, regarded all names based on Central American material of the group available at that time to be synonyms, but he reluctantly continued to recognize *E. gulosus* as valid.

Taylor (1952), in his monograph of Costa Rican anurans, recognized *Eleutherodactylus rugosus* (pp. 730–734) and *E. florulentus* (pp. 765–766) as valid species. He accepted Noble's (1918) synonymy of *Lithodytes megacephalus* with *E. rugosus*, but questioned whether *L. gulosus* and *L. pelviculus* should be included there.

Savage (1973, 1976, 1980) and Savage and Villa (1986), influenced by Dunn's unpublished synonymy, regarded all Central American names for this group to be based on specimens of *E. biporcatus*. Myers and Rand (1969) and Rand and Myers (1990) followed Dunn (1931) in using *E. biporcatus* for Panamanian members of this group. Lynch (1975), in the most recent review of the taxonomy of these frogs, likewise concluded that these various names represented only one species in Central America, namely *Eleutherodactylus biporcatus*. He included that species in his *Eleutherodactylus bipor-*

[5] A South American broad-headed frog unrelated to the *biporcatus* group but confused with it is the nominal *Limnophys napaeus* Jiménez de la Espada, 1870, which authors have placed in the synonymy of *Eleutherodactylus biporcatus*. Lynch (1975: 30–31) reviewed the evidence and allocated *napaeus* to the synonymy of *Eleutherodactylus cornutus* in the *sulcatus* species group.

catus group along with *E. cerastes*, *E. cornutus*, and *E. necerus* of northwestern and upper Amazonian South America, and *E. bufoniformis* of lower Central America and northwestern South America, but he placed the Venezuelan *E. maussi* in the separate *sulcatus* group. This grouping was reiterated in Lynch's (1976) discussion of the South American species groups of *Eleutherodactylus*.

Lynch (1975, 1976) regarded the forms in his *E. biporcatus* group as closely related since they shared the features of very broad heads (head width > 42% SVL), finger I > finger II, and smooth venters. Lynch (1975) indicated that another cluster of broad-headed South American *Eleutherodactylus*, the *sulcatus* group, was somehow related to the *biporcatus* group, but in the 1976 paper he placed the two groups in different infrageneric units within the genus.

Subsequently, Lynch (1981) expanded the *sulcatus* group to include the nominal monotypic genus *Amblyphrynus* (Cochran and Goin, 1961) and a new form to bring its composition to five species: *Eleutherodactylus helonotus* (Ecuador), *E. ingeri* (Colombia), *E. maussi* (Venezuela), *E. ruizi* (Colombia), and *E. sulcatus* (Amazonian Ecuador and Peru).

Savage and DeWeese (1979, 1981) and Savage (1984, 1987), while acknowledging the utility of Lynch's (1976) attempt to bring some kind of order to the classification of *Eleutherodactylus*, criticized Lynch's system as essentially phenetic and based on trivial external features much given to homoplasy. They preferred to emphasize the condition of jaw muscles and karyology over finger length and ventral texture.

Lynch (1986) responded to this challenge with a thorough examination of the jaw muscle characters of the m. adductor mandibulae of *Eleutherodactylus*, first discovered by Starrett (1968) and touted by Savage and DeWeese (1979, 1981) as systematically informative. Lynch's work has broad significance to the systematics of all *Eleutherodactylus* and their allies, but only those aspects relating to the present paper are summarized here.

The principal result of Lynch's 1986 study was the recognition of two major clades within the genus. The South American clade is characterized by having a m. adductor mandibularis posterior subexternus present, and the mandibular ramus of the trigeminal nerve (V3) passing external (lateral) to the muscle ("S" condition). The Central American clade (subgenus *Craugaster* Cope, 1862: 153) has a m. adductor mandibularis externus superficialis, and the trigeminal nerve passing mediad (internal) to the muscle ("E" condition). This conclusion required a complete renovation of the two broad-headed species groups, because only *Eleutherodactylus biporcatus* (sensu lato), *E. bufoniformis*, *E. florulentus*, *E. necerus*, and *E. maussi* have the E condition; these were assigned to the *biporcatus group*. Except for *E. maussi*, the remaining South American broad-headed forms all have the S condition and currently are placed in the *sulcatus* group.[6]

In 1980, Jonathan A. Campbell collected several *biporcatus*-like frogs from the mountains of eastern Guatemala. Savage examined this material in 1980 and expressed his opinion that it was doubtless a diminutive new member of the *biporcatus* group. Campbell (1994), after obtaining additional material, described the species as *Eleutherodactylus aphanus*.

Lynch and Duellman (1997), in a major treatment of *Eleutherodactylus* relationships, placed *Eleutherodactylus bufoniformis* and *E. necerus* in a separate *bufoniformis* species group, leaving the *biporcatus* group with three recognized species (*aphanus*, *biporcatus*, *maussi*). We accept the *biporcatus* and *bufoniformis* species groups for purposes of the present study, which focusses on the first group.

REDISCOVERY OF *LITHODYTES GULOSUS*, COPE, 1875

In February of 1976, Myers collected a series of unusual juvenile *Eleutherodactylus* (fig. 1) in leaf litter near the site of the pre-

[6] The *sulcatus* species group now includes nine species according to the latest revision (Lynch, 1997). It is a South American assemblage. Only one species occurs (barely) in political Central America, namely *E. laticorpus* Myers and Lynch (1997) from the Panamanian-Colombian frontier.

Fig. 1. The first specimen collected during the rediscovery of *Lithodytes* [*Eleutherodactylus*] *gulosus* in 1976—a century after its original description (Cope, 1875)—at the proposed Fortuna Dam site in western Panama. A juvenile female (AMNH 95035) of 32 mm SVL, less than half grown; note the pustulate dorsum, a juvenile condition (compare adult in fig. 12). [From a transparency by C. W. Myers.]

sent-day Fortuna Dam (then being surveyed for construction), at 1120 m, on the Pacific versant of western Panama (fig. 2). Although reminiscent of the common broad-headed juveniles identified with *Eleutherodactylus biporcatus*, they differed from them most obviously in lacking well-defined dorsal plicae and in having a different ventral coloration. In addition, the dorsum was conspicuously covered by numerous small pustules. Direct comparison with juvenile *E. biporcatus* of the same size strongly suggested that these frogs were not conspecific with typical lowland *E. biporcatus*.[7]

Later visits to nearby areas by Myers and John Daly in July of 1982 and January 1983 led to the capture of two large females, one subadult female, and additional juveniles of this enigmatic frog. Found at elevations between 1000 and 1220 m, on and near the continental divide, the adults were distinct from lower-elevation *E. biporcatus* in lacking dorsal plicae and in details of coloration. The question then naturally arose as to whether these frogs represented an undescribed species or were conspecific with one of the several taxa previously named from western Panama and southern Costa Rica, but then regarded as junior synonyms of *E. biporcatus*. Crucial to resolving this question was examination of the type specimens of each available name. Consequently, Myers borrowed the type series of *Strabomantis biporcatus* and the holotype of *Hylodes rugosus* from the Berlin Museum. A preliminary comparison of these animals with the newly collected material left him with little doubt that the Fortuna frogs could not be associated with either of the species represented by the Berlin types.

But Myers was astonished to find that the type series of *S. biporcatus* represented a species different from the frogs usually called *E. biporcatus* for more than half a century, and that they were also unlike any other known species from Central America. This puzzlement led to consultation with Savage on the occasion mentioned in the introduction to this paper, with the latter fully agreeing with Myers' conclusions that the Fortuna frogs: (1) were not conspecific with the species usually called *E. biporcatus* in Central America; (2) were not conspecific with the types of *S. biporcatus* or *H. rugosus*; (3) and that the types of *S. biporcatus* were not representatives of the species usually referred to as *E. biporcatus* in Central America!

Further discussion led us to the hypothesis that the Fortuna frogs might well be examples of one of the other of Cope's nominal species, *Lithodytes gulosus* or *L. megacephalus*, also from an upland area in the same mountain range as Fortuna but on the Atlantic slope in southern Costa Rica. The possibility also existed that both these names were based on a single taxon conspecific with the Fortuna examples.

Cope's (1875: 110–112) original descriptions clearly differentiated the holotypes of *Lithodytes gulosus* and *L. megacephalus* as follows:

[7] Jungfer (1988: 16) later used the name *Eleutherodactylus biporcatus* for a juvenile specimen from the Fortuna regional population, but his accompanying photograph represents a species (*E. megacephalus*) from another locality.

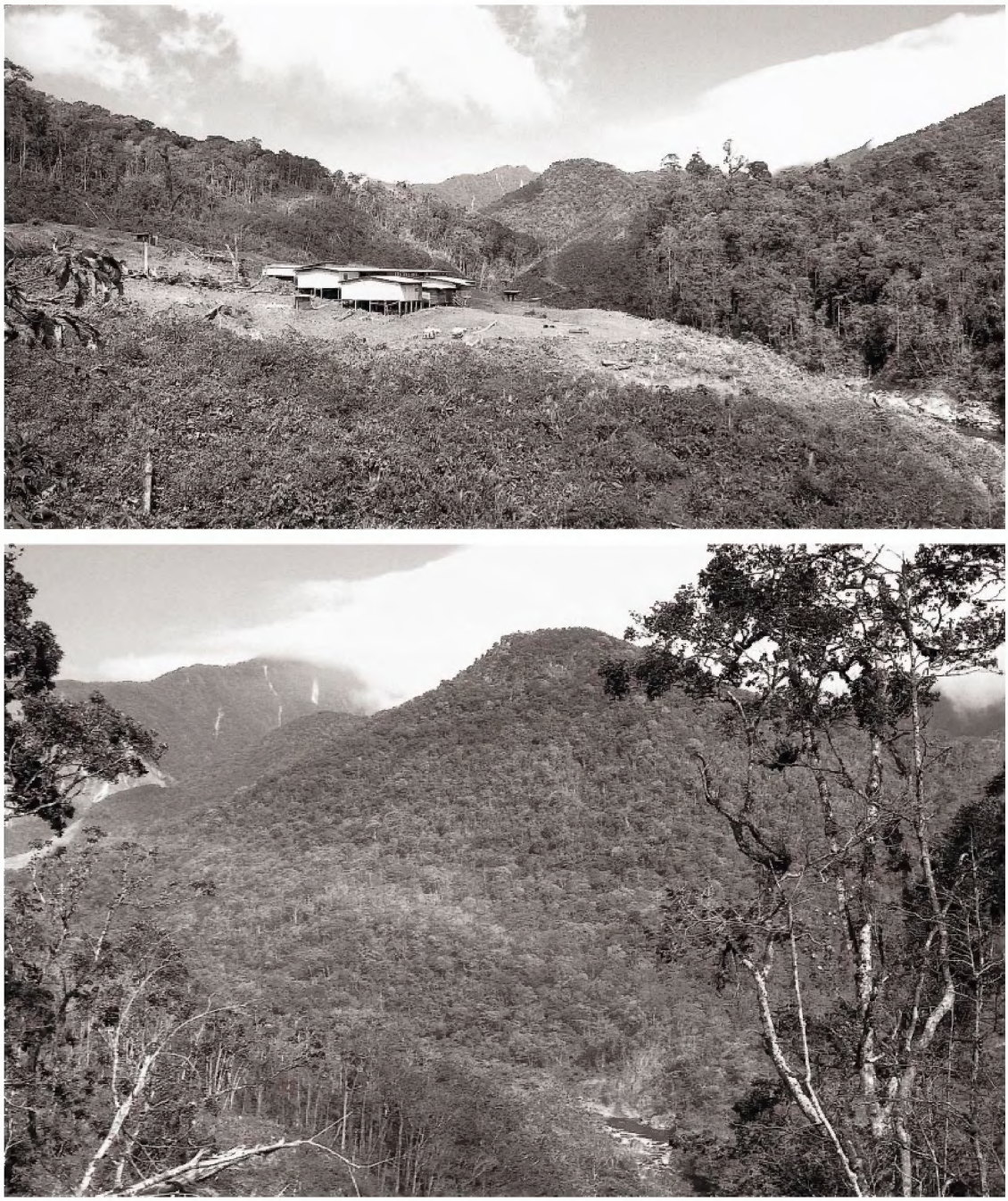

Fig. 2. Views of the Fortuna Dam site in the upland valley of the Río Chiriquí, in 1976, prior to road and dam construction (access was by trail or helicopter). **Upper:** Survey and research camp of the Instituto de Recursos Hidráulicos y Electrificación (IHRE) above Río Chiriquí (at right), on northern base of Cerro Fortuna, about 1000 m above sea level. **Lower:** View looking westward across the subsequently flooded Río Chiriquí to Cerro Pinola (center), from 1060 m on north slope of Cerro Fortuna. [Photographs by C. W. Myers, March 2–3, 1976.]

L. gulosus	*L. megacephalus*
No dermal plicae	Dermal)(folds dorsally and laterosacral plicae present
Dorsum uniform dark leather brown	Dorsum light ash
Posterior thigh like dorsum	Posterior thigh black, marbled distally with ash, black continuing as patch to vent
Head width 2.2 times in head-body length (SVL); 46% of SVL	Head width 2 times in SVL; 50% of SVL
Adult female 103 mm SVL	Adult female 70 mm SVL

The types of both putative species are housed at the United States National Museum of Natural History and are part of the W. M. Gabb collection made in Costa Rica in 1873–1874. The holotype of both *Lithodytes gulosus* (USNM 32590) and of *Lithodytes megacephalus* (USNM 32579) are from "Pico Blanco", Limón Province, Costa Rica, 6000 ft. However, as pointed out by Savage (1970), Gabb's expedition did not ascend Pico Blanco (= Cerro Kamuk), but actually climbed to the summit of Cerro Utyum, the next peak to the northwest.

The type specimen of *Lithodytes gulosus* is in excellent condition and agrees well with Cope's original description. Unfortunately the type of *Lithodytes megacephalus* has suffered serious decay and today consists only of skin fragments and disarticulated bones. The maceration of this specimen is relatively recent, as Noble (1918) and Dunn (unpublished notes) examined it while it was still whole. Noble regarded the specimen as a large adult conspecific with *Eleutherodactylus rugosus* and slightly different from the type of *L. gulosus*, which he retained as *Eleutherodactylus gulosus*. Dunn (1931) apparently considered both names as synonyms of *Eleutherodactylus biporcatus*, the types of which he had examined in Berlin in 1928.

Although the condition of the holotype of *Lithodytes megacephalus* makes direct comparisons impossible, Cope's (1875) description and illustration (reproduced herein as fig. 6) clearly demonstrate that it is not conspecific with the adult Fortuna frogs. Unlike them it had well-developed suprascapular and laterosacral ridging, the posterior thigh surface was black, marbled distally with ash, and the dark seat patch was continuous onto the lower posterior surface of the thigh.

Comparison of the holotype of *Lithodytes gulosus* with the two adult females (AMNH 124370, AMNH 124372), 84 and 72 mm SVL, respectively, and a subadult female (AMNH 124371, 46 mm SVL) from the Fortuna Dam area of Panama leaves little doubt that they represent the same species. The most striking similarity is the absence both of the suprascapular plicae and the laterosacral tubercle and/or ridge system. The plicae are characteristic of all other named forms of *biporcatus*-like frogs, and laterosacral tubercles or ridges are found in some of the other species of the group (fig. 3).

In other features, the adult females from Panama agree closely with the holotype and Cope's description of *Lithodytes gulosus* in having a uniform dark dorsum and posterior thigh surface. In addition they have the chin and throat pale or gray-brown, pale venters mottled with gray-brown or with dark brown spotting, and the seat patch is inconspicuous.

The subadult female differs from the others in some features of coloration, including distinct transverse dark bars on the limbs, some pale tan spotting on the posterior thigh surface, the dark seat patch mark restricted to the area around the vent, the chin and throat gray with small white spots, the underside of the leg suffused with yellow, and the venter, groin and anterior thigh surface marbled blackish gray on white (life colors). This specimen is somewhat intermediate in coloration and dorsal pustulation between the large adults and the series of juveniles.

Unlike adults, juveniles (AMNH 95035–95046, 124365–124369; 18–32 mm SVL) have dorsally pustulate skin, a lighter dorsum with obscure darker mottling, and greenish ventral coloring; juveniles also differ notably from adults in that traces of suprascapular plicae can be discerned on close examination in most specimens (fig. 13). A juvenile male

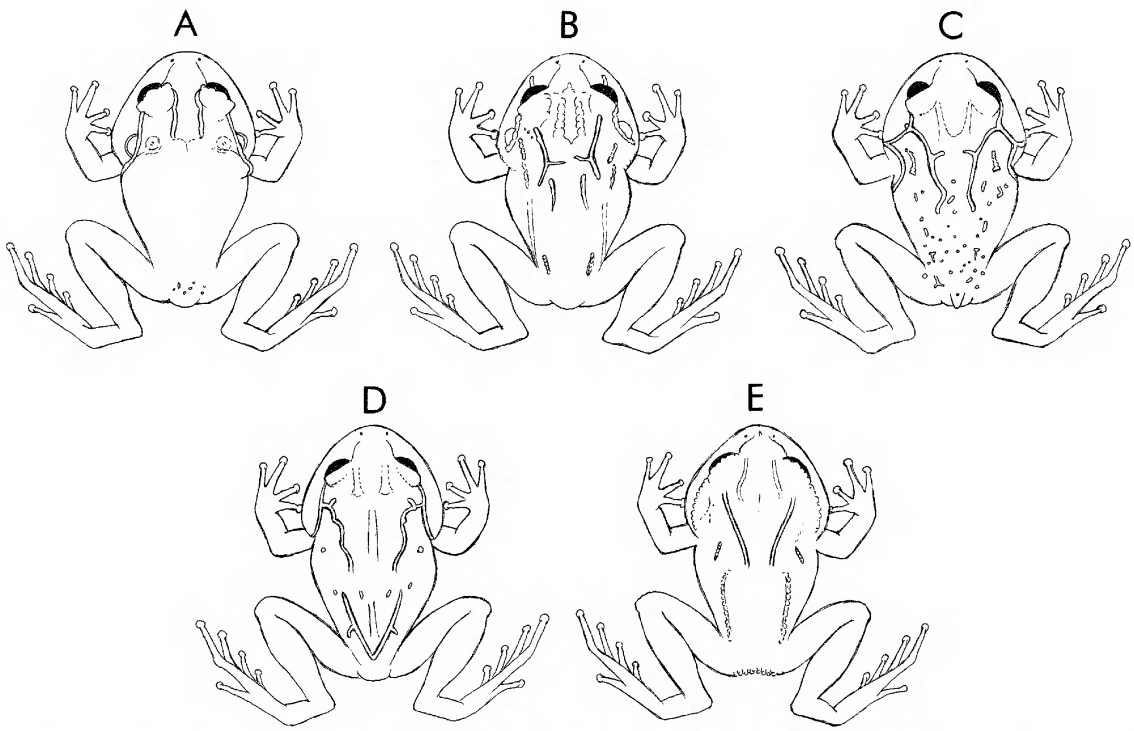

Fig. 3. Diagrammatic representation of dorsal-ridge patterns in the *Eleutherodactylus biporcatus* group. **A:** *E. gulosus*, no definite dorsal plicae in adults (although weak, short anterior suprascapular plicae are discernible in most juveniles; see fig. 13). **B:** *E. biporcatus* s.s. (*maussi* auctorum), paired suprascapular and weak laterosacral plicae. **C:** *E. rugosus*, paired suprascapular plicae, no laterosacral plicae. **D, E:** *E. megacephalus* has chalice-shaped or hourglass-shaped suprascapular plicae, with geographic variation in the laterosacral plicae or linear series of closely set tubercles; the V-shaped laterosacral pattern (D) is common from Nicaragua through Costa Rica, tending to be replaced in western Panama by nonconverging (E) parallel ridges. Two additional species, *Eleutherodactylus aphanus* (fig. 8) and *E. opimus* (figs. 17–19), resemble *E. rugosus* (C) in lacking paired laterosacral plicae or tuberculate ridges, although these species are overall much less tuberculate than *rugosus* (fig. 20).

(KU 115221, 28 mm SVL) from the Atlantic versant of Panama (juncture of Río Claro and Río Changena, Bocas del Toro, 910 m) also appears to be conspecific with the holotype and Fortuna Dam series; it has a pustulate dorsum and resembles the subadult female in coloration.

We conclude that there can be little doubt that the Costa Rican holotype of *Lithodytes gulosus* and recent specimens from western Panama represent a species distinct from all related broad-headed *Eleutherodactylus*; it is the only one in which dorsal ridging is completely lacking (adults) or very vague (juveniles). In addition, this species attains a much larger size than any other broad-headed form (table 2). Features of juvenile and adult coloration are also different from those found in allied forms (see Systematic Synopsis) further supporting recognition of *Eleutherodactylus gulosus* (Cope, 1875) as a valid species.

IDENTITY OF *STRABOMANTIS BIPORCATUS* W. PETERS, 1863

The syntypic series of *Strabomantis biporcatus* consists of four specimens, ZMB 3330 (3 adults) and ZMB 3322 (a juvenile), all purportedly from "Veragua". The adults, hereafter referred to as ZMB 3330A, B, and C, are about 67, 60, and 55 mm SVL and the juvenile is 32 mm (fig. 4).

These frogs resemble the several broad-headed *Eleutherodactylus* described from Central America in having cranial crests on

Fig. 4. The type series of *Strabomantis biporcatus* W. Peters, 1863, in dorsal and ventral view. Left to right: ZMB 3330[A]♀, 3330[B]♀ (lectotype), 3330[C](sex?), 3322 juv. The type locality was given as ''Veragua'' (western Panama), but based on current knowledge, these specimens must have been collected in Venezuela.

TABLE 1
Measurements (in mm) Made a Century Apart on the Two Largest Syntypes of *Strabomantis biporcatus* Peters, 1863

	Peters, 1863		Remeasured 1997	
	A	B	A	B
Total length [SVL]	75	62	67[a]	60
Head length [diagonal]	25	22	25.2	24.5
Head width	35	31	33	31.5
Anterior corner of eye to snout	10	8.5	10	9
Posterior corner of eye to snout	18.5	16	18	16
Hind leg	45	39	47	44
Hind leg distance from snout	110	110	111	103

[a]These probably shrunken specimens are flaccid, which increases the extent of normal measuring error that is inherent with soft-bodied creatures. Our repeated total length (SVL) measurements varied from 63 to 67 mm for specimen A, and 59 to 61 mm for specimen B.

the frontoparietal bones, and resemble all except *E. gulosus* in the presence of well-developed suprascapular plicae. They differ most obviously from any broad-headed *Eleutherodactylus* known from the region in having a tarsal fold, greatly enlarged, conical subarticular tubercles under the fingers, and definite plantar tubercles.

Because of these discrepancies, we considered the possibility that some mix-up in data had occurred, given the former custom at the Berlin Museum of having the identification and specimen number on a slip of paper placed in the bottle but unattached to the specimens. However, direct comparison of the syntypes with Peters' (1863) description revealed no essential difference between them. Peters gave measurements for the largest examples, which he listed as "A" and "B", and we remeasured the largest syntypes (ZMB 3330A, 3332B) as shown in table 1.

In view of the length of time in preservative and the present softened condition of the specimens, these measurements are in reasonable agreement. This, in combination with the close concordance between other characteristics of these specimens and the original description, convinces us that they are the syntypes of *Strabomantis biporcatus* as labeled. At this point, we recalled the situation described above under Taxonomic History, where erroneous locality data involved two other names based on Berlin Museum specimens: *Phrynidium crucigerum* Lichtenstein and von Martens 1856, and *Hylodes gollmeri* W. Peters, 1863, originally described from Veragoa and Caracas, respectively. Subsequent research (Rivero, 1961; Savage, 1987) demonstrated that some of the syntypes of the former *Atelopus cruciger* and the type of *Eleutherodactylus gollmeri* were conspecific with a Venezuelan and a Central American species, respectively.[8]

Aided by this clue, we compared the syntypes of *Strabomantis biporcatus* with *Eleutherodactylus maussi* Boettger, 1893, the only known broad-headed species of the genus in Venezuela. And indeed, specimens from a series (AMNH 70533–70552, 70554–70558) of *E. maussi*, along with the redescription of that form by Lynch (1975), agreed in every significant feature with the syntypes of *Strabomantis biporcatus* (fig. 5). Significant characters included: large size (adult females about 49–74 mm SVL),

[8] But as already discussed (footnote 4) Lötters et al. (1998) chose a presumed syntype of *Phrynidium crucigerum* from Panama as "lectotype" and placed the name in the synonymy of *Atelopus varius*, unfortunately leaving the name *cruciger* as unavailable for Venezuelan populations. (Added in press: Lötters and La Marca [*Bull. Zool. Nomencl.* 58: 119–121, June 2001] have now petitioned to conserve the name *Atelopus cruciger* through selection of a neotype, collected in 1930, that is not part of the original type series.)

Fig. 5. The South American frog heretofore known as *Eleutherodactylus maussi* (Boettger, 1893). Left to right: AMNH 70539, 70552, 70556, adult females from Rancho Grande in the Coastal Range of northern Venezuela. Compare with the syntypes of the earlier named *Strabomantis biporcatus* W. Peters, 1863, in figure 4.

slightly arched vomerine odontophores, a suprascapula and paravertebral ridge system, laterosacral tubercle or ridge system prominent to absent, conical subarticular tubercles under the fingers, an inner tarsal fold, weak toe fringes, low inner and prominent outer metatarsal tubercles, and planter tubercles present.

At first glance, the only apparent point of disagreement between the syntypes of *Strabomantis biporcatus* and definitive *Eleutherodactylus maussi* involved the texture of the ventral integument. *Eleutherodactylus maussi* is characterized by having the abdominal surface coarsely granular or areolate. In his original description of *S. biporcatus*, Peters (1863: 406) noted that "der Körper erscheint glatt, ist aber bei genauerer Betrachtung allenthalben mit kleinen Wärzchen bedeckt . . . Eben so zeigt die Bauchseite kleine Wärzchen, während die Kehle glat ist". [The body seems smooth, although . . . very small knobs can be discovered . . . The ventral side exhibits no small knobs, while the throat is smooth.] Peters mentioned that the *kleinen Wärzchen* (small warts, tubercles, or knobs) were denser and somewhat larger on the posterior thigh, suggesting that he was not differentiating coarse granules from other small knobs or tubercles found on the body.

Although the three adult syntypes superficially appear to have smooth ventral surfaces, close examination reveals traces of coarse granulation on the venters. The skin on the throat is smooth in the largest specimen, as stated by Peters, but is coarsely granular on the other two. The juvenile has an obviously coarsely-granular venter but a smooth throat. The condition of ventral granulation frequently is distorted by preservation, especially if the frog was originally poorly fixed in weak alcohol (modern formalin preservation also often tends to diminish granulation). Our judgement is that all the syntypes had the venters areolate (coarsely granular) in life.

Although no collector is identified by Peters (1863) in the original description, the Berlin Museum catalog lists the source as Warszewicz, who also was responsible for Panamanian syntypes of *Atelopus cruciger*, a name also applied to a Venezuelan frog (footnotes 4, 8, and associated text). Curator Rainer Günther provided the following in-

formation (in letter to Myers, September 27, 1995):

> [Some of] the types of *Atelopus cruciger* were indeed collected by the same collector named Warszewicz . . . as [were] the types of *Strabomantis biporcatus* . . . In our archives we found a report by Lichtenstein saying that he (obviously personally) purchased from Warszewicz "6 Gläser mit verschiedenen Tieren in Weingeist, die er auf der Cordillera von Veragoa in bisher noch gar nicht besuchten Thälern gesammelt zu haben erkläart". From the listed specimens (some clearly with marine origin) however it becomes clear that Warszewicz obtained his material not only in Veragoa (sometimes Veragua) but also from elsewhere. Some archivist noted on the deed of Warszewicz already: Panama, Brasilien and Peru. . . . From our documents it follows further that most (?) of the Warszewicz collection was sold by auction in the British Museum . . . In our herpetological collections Catalogue all the specimens obtained from Warszewicz have as collection site Veragoa or Veragua, which after all is not always correct.

The agreement of the syntypes of *Strabomantis biporcatus* and representatives of the nominal taxon *Eleutherodactylus maussi* in all diagnostic features forces us to conclude that *biporcatus* is not a Central American frog as long assumed. The proper name for the Venezuelan species must be *Eleutherodactylus biporcatus* (Peters, 1863) under the principle of priority (International Commission on Zoological Nomenclature, 1999: art. 23). The name *maussi* is little used, and its replacement will not lead to significant destabilization in nomenclature.

APPLICATION OF THE NAME *LITHODYTES MEGACEPHALUS* COPE, 1875

The discovery that *Strabomantis biporcatus* is a senior subjective synonym of *Hylodes maussi* not only requires that the Venezuela species be known as *Eleutherodactylus biporcatus*, but has another major taxonomic repercussion as well. For 70 years, following Dunn (1931), the name *Eleutherodactylus biporcatus* has been applied almost universally to common lowland broad-headed frogs that occur from Honduras to Colombia. With the recognition that *Eleutherodactylus gulosus* is a valid upland species, four other names are potentially applicable to the lowland frogs. These are: *Hylodes rugosus* Peters, 1873; *Lithodytes megacephalus* Cope, 1875; *Lithodytes pelviculus* Cope, 1878; and *Lithodytes florulentus* Cope, 1893.

As we will show in a later section, the holotypes of the first, third, and fourth names are based on an essentially allopatric Pacific population confined to the humid forests of southwestern Costa Rica and adjacent southwestern Panama. Our evidence establishes this population as a valid species. This raises the questions as to whether the name *Lithodytes megacephalus* is an available name based on a specimen from an Atlantic slope population in Central America.

As previously pointed out, the holotype of *Lithodytes megacephalus* (USNM 32579)[9] from the Atlantic versant of Costa Rica is in such a deteriorated condition as to defy further study. Nevertheless, the original description and figure (Cope, 1875: 110–113, pl. 23, fig. 11, 11a) leave little question that it represents Atlantic versant frogs long referred to as *Eleutherodactylus biporcatus*. The principal features supporting this conclusion are the presence of well-developed suprascapular and laterosacral ridging (fig. 6), the posterior thigh surface black, marbled with ash, with the black pigmentation essentially continuous to the vent (fig. 6), the light dorsal color, and the size (70 mm SVL). All other features described or figured by Cope are consistent with this conclusion. In addition, Noble (1918) and Dunn (1931) both examined the holotype while it was in good condition and concluded that it was conspecific with frogs fitting their concepts, respectively, of *Eleutherodactylus rugosus* and *E.* "*biporcatus*" in Central America.

A problem with this interpretation centers on the elevational data associated with the holotypes of both *Lithodytes megacephalus* and *Lithodytes gulosus*. Cope stated that the former was collected "on a spur of Pico Blanco, at 6000 feet elevation" and the latter "from the same locality as the last species." As previously pointed out (Savage, 1970), the Gabb expedition that collected both specimens actually climbed Cerro Utyam, not

[9] Savage (1970) either through a lapsus calami or typographical error listed Cope's type of this species as *Hylodes megalocephalus*. This stands as an incorrect subsequent spelling of the species name, and it has no status in nomenclature.

Fig. 6. Original illustration of the holotype of *Lithodytes megacephalus*, reproduced same size from Cope's (1875) figures 11 and 11a on plate 23 (= pl. "1" in fig. legends on page facing pl. 23).

Pico Blanco (Cerro Kamuk), the next peak to the southeast.

The elevation of 6000 ft (1829 m) is well above the known limit for nominal *Eleutherodactylus* "*biporcatus*" on the Atlantic slope. On the other hand that elevation may well be within the range for *Eleutherodactylus gulosus*, which we now know occurs at least between 1000 and 1220 m. We do have some question as to whether they both are found as high as 1830 m but it is possible that they are marginally sympatric at a lower elevation.

It is not altogether clear to us from the original descriptions that Cope's statement that the holotype of *Lithodytes gulosus* being "from the same locality. . . " as the type of *L. megacephalus* meant anything more than that they were both collected on Cerro Utyam. However, the USNM catalog lists both as being from "Pico Blanco, Costa Rica, 6000 ft." Savage (1970) also listed both as from "spur of Cerro Utyam, 6000 ft. (1830 m)". We now suspect that Gabb's figure of 6000 feet is an overestimate of the elevation where the specimen of *L. megacephalus* was taken, and that while both holotypes are from the same locality (Cerro Utyam) in a loose sense, they probably were not collected at the same place.

In spite of the perceived difficulty associated with the elevational data, we are convinced on the basis of available evidence that the name *Eleutherodactylus megacephalus* (Cope, 1875) is the valid name for many frogs referred previously to *E. biporcatus* (sensu Dunn) in lower Central America. Even so, as demonstrated in this paper, the previous "*biporcatus*" auctorum was a composite of *at least* three species. Even as restricted herein, *Eleutherodactylus megacephalus* may still be a composite (see species account under Remarks).

RESURRECTION OF *HYLODES RUGOSUS* W. PETERS, 1873

The holotype of *Hylodes rugosus* (ZMB 7812; fig. 7) is a subadult, 21 mm SVL, having prominent suprascapular ridging, no laterosacral rows of tubercles, a pair of distinct broad dorsal stripes, vivid black and light thigh bars, and a contrasting pattern of light and black groin markings. In all these fea-

Fig. 7. Holotype of *Hylodes rugosus* W. Peters, 1873. ZMB 7812 in dorsal and ventral view, a juvenile from "Chiriqui", western Panama. Scale divisions = mm.

tures, which in combination differentiate it from *Eleutherodactylus gulosus* and *E. megacephalus*, it closely resembles samples of broad-headed frogs of this complex from the Golfo Dulce region of southwestern Costa Rica and adjacent Panama. Although the type locality "Chiriqui" is ambiguous because it was applied to both Atlantic and Pacific versant Panama at the time of the species' description, the holotype is obviously from the Pacific slope population. Examination and comparisons with material from the Golfo Dulce of the holotypes of *Lithodytes pelviculus* Cope, 1878 (26 mm SVL) and the description of *Lithodytes florulentus* Cope, 1893 (type lost but 35 mm SVL) show that these names are synonyms of *L. rugosus*. All examples from southwestern Costa Rica share the features mentioned above except that the light (reddish brown in life) dorsal stripes are occasionally absent. The vivid black and light (scarlet in life in adults) thigh and groin markings are a particularly distinctive feature.

The Golfo Dulce series and *E. megacephalus* most closely resemble one another within the *biporcatus* group in general habitus and in having well-developed suprascapular plicae. In the Golfo Dulce frogs, most individuals have a well-developed medially directed branch from the anterior arm of each suprascapular ridge, but this is never seen in *E. megacephalus*. In addition, the upper surface of these frogs is covered by many relatively large wartlike pustules, while the pustules present in juvenile *E. megacephalus* are small and tend to be pointed, with the dorsum of adults being smooth to shagreened with only a few widely scattered pustules. *Eleutherodactylus megacephalus* also has paired laterosacral series of pustules that are usually fused into ridges, which are lacking in Golfo Dulce material. Most frogs in the last sample have distinctive paired broad dor-

sal stripes, which are never present in *E. megacephalus*.

Since the Golfo Dulce population is completely allopatric to those here assigned to *Eleutherodactylus megacephalus*, and there is no evidence of intergradation in the characteristics distinguishing them, we conclude that two species are represented. Consequently we recognize *Eleutherodactylus rugosus* (Cope, 1893) of the Pacific slope of southwestern Panama and adjacent Costa Rica as a valid species within the *biporcatus* group.

SYSTEMATIC SYNOPSIS: THE *BIPORCATUS* SPECIES GROUP

INCLUDED SPECIES: *Eleutherodactylus aphanus* Campbell, 1994; *E. biporcatus* (W. Peters, 1863); *E. gulosus* (Cope, 1875); *E. megacephalus* (Cope, 1875); *E. opimus*, new species; and *E. rugosus* (W. Peters, 1873). See table 2 for a tabular comparison of the included species.

DEFINITION: Robust, toadlike eleutherodactylines with broad heads (head width 39–55% of SVL in adults, usually > 42%) having paired frontoparietal crests that are visible externally in adults of most species; head outline from above semicircular or ovoid to broadly rounded; upper eyelids tuberculate; tympanum external, distinct, annulus tympanicus prominent, round in males, ovoid and higher in females; supratympanic fold from eye towards arm; no inguinal glands; no male nuptial pads; vomerine odontophores triangular, or slightly arched lying posterior and medial to large choanae, the patches narrowly separated medially; tibia 46–60% of SVL; disks present on all digits, not expanded on fingers, slightly expanded on toes; fingers short, slender; relative length of appressed fingers III > I ≥ II ~ IV; basal toe webbing absent or very slight; relative length of appressed toes IV > III > V > II > I, the third much longer than fifth; jaw muscle formula DFSQAT + e.

KARYOLOGY: 2N = 20; N.F. = 36 in two examined species (*Eleutherodactylus megacephalus* and *E. opimus*), and 2N = 20; N.F. = 38 in two other species (*E. gulosus* and *E. rugosus*). In *Eleutherodactylus biporcatus*, the karyotype is 2N = 36 in females and occasional males (18 pairs of chromosomes), and 2N = 35 in most males (16 pairs and 3 unpaired chromosomes); N.F. = 42. See figure 21 and closing discussion.

KEY TO SPECIES

1. Venter smooth; no tarsal fold; no vocal slits in adult males; dorsal plicae present or absent 2
   Venter coarsely areolate; an inner tarsal fold present; vocal slits in adult males; paravertebral plicae at midbody separate from suprascapular plicae (fig. 3B). . . . . *E. biporcatus*
2. Dorsum of adults and juveniles with distinct paired suprascapular plicae (figs. 3C–3E, 18). 3
   Dorsum of adults lacking suprascapular plicae (fig. 3A), but characteristically configured, weakly developed anterior plicae present in most juveniles (fig. 13) . . . . . *E. gulosus*
3. Posterior dorsum lacking laterosacral system of either V-shaped or parallel plicae or closely set tubercles (e.g., figs. 3C, 18) 4
   Posterior dorsum with a definite laterosacral system of either V-shaped (fig. 3D) or nonconverging (fig. 3E) parallel rows of tubercles or tuberculate ridges . . . . . *E. megacephalus*
4. Posterior surface of thighs not contrastingly marked with black and red (or white), although sometimes barred in black with tan interspaces; dorsum smooth or with scattered low pustules 5
   Posterior surface of thighs contrastingly marked with black bars, separated by red interspaces (white in juveniles) in life; dorsum strongly tuberculate with numerous large warts and ridges. . . . . *E. rugosus*
5. Venter immaculate; size small, adult males 18–22 mm SVL, adult females 35–44 mm . . . . . *E. aphanus*
   Venter variously marked with brown and/or large light spots; size moderate to large, adult males probably >30 mm SVL, adult females to at least 69 mm . . . . . *E. opimus*

Eleutherodactylus aphanus Campbell

Figures 8, 9 (map)

Eleutherodactylus aphanus Campbell, 1994: 296–302, figs. 1–3. Holotype: UTA A-33405, an adult male from 12.0 km WSW Puerto San-

TABLE 2

Characteristics of the *Eleutherodactylus biporcatus* Group[a]

Character	*aphanus*	*biporcatus (maussi)*	*gulosus*	*megacephalus*	*opimus*	*rugosus*
SVL mm ♂	18–22	30–38	?	30–43	?	27–44
♀	35–44	49–74	72–103	50–70	69	35–65
Suprascapula plicae	present	present	present only in juveniles	present	present	present
Paravertebral plicae	absent	present	absent	absent	absent	absent
Laterosacral plicae or linear rows of tubercles	absent	present	absent	present	absent	absent
Venter	smooth	coarsely areolate	smooth	smooth	smooth	smooth
Odontophores	triangular	slightly arched	triangular	triangular	triangular	triangular
Subarticular finger tubercles	low	projecting	low	low	low	low
Inner tarsal fold	absent	present	absent	absent	absent	absent
Toe keels or fringe	weak	weak	none	none	none	none
Inner metatarsal tubercle	large, oval	large, oval	large, oval	large, oval	large, oval	large, oval
Outer metatarsal tubercle	small, low	small, low	small, low	small, low	small, low	small, low
Plantar tubercles	absent	present	absent	absent	absent	absent
Male vocal slits	absent	present	?	absent	absent?	absent
Average tympanum size	♂ > ♂	♂ > ♂	♂≥♀	♂ > ♀	♂ > ♀	♂ > ♀
Adult ventral color pattern	patternless, ♀ gray or purple ♂ yellow to chartreuse	mottled or small white spots	mottled brown and white	variable, usually brown reticulum and yellowish spots	brown reticulum, small or large white spots	dark brown reticulum, large white spots
Hue in life of pale ventral area(s) in juveniles	immaculate white?	?	bright greenish yellow	yellow to red-orange, or grayish[b]	whitish	orange-red to red

TABLE 2
Continued.

Character	*aphanus*	*biporcatus (maussi)*	*gulosus*	*megacephalus*	*opimus*	*rugosus*
Groin and anterior thigh	like venter	like venter	like venter	similar to venter	variable, uniform or mottled, thigh barred or not	dark reticulum with vivid white spots
Posterior thigh	white, purple, or tan, with brown reticulation	brown with many tiny pale spots	uniform gray or obscurely barred or spotted	variably spotted or mottled light and dark	black or brown, with or without gray areas	alternating black and red bars (white in juvenile)
Dark seat patch	continuous onto thigh	around vent	around vent	continuous onto thigh	continuous onto thigh	continuous onto thigh

[a] This table indicates some species differences but does not adequately reflect intraspecific variation, the study of which is made difficult by the paucity of adults, which are absent or rare in most population samples.

[b] Geographically variable, possibly two species.

to Tomás, Department of Izabal, Guatemala, 786 m.

DIAGNOSIS: This, the smallest member of the *biporcatus* group (fig. 8), is distinguished from its allies by the combination of an immaculate venter, presence of suprascapular plicae, and lack of laterosacral ridges or tubercle series. *Eleutherodactylus aphanus* is most similar to *E. opimus*, but differs in ventral coloration, and *aphanus* may also differ in having weakly keeled digits (Campbell, 1994: 298).

MORPHOLOGY: Adult males 18–22 mm SVL, adult females 35–44 mm (mean SVL = 19.8 mm, 4 ♂, 40.2 mm, 3 ♀); tibia 48–58% of SVL; head width 45–50% of SVL; cranial crests present, visible externally in some adult females; dorsal surfaces basically smooth; definite suprascapula plicae forming a chalice- or hourglass-shaped system; flanks smooth; no definite laterosacral system of tubercles or ridges; snout outline from above ovoid; nostrils not protuberant; upper eyelid with one to several tubercles; width less than IOD; tympanum large, about 70–90% of eye length in males, 50–70% in females; vomerine odontophores triangular, lying posterior and mediad to large choanae; patches narrowly separated medially; subarticular tubercles ovoid, obtuse; thenar tubercle low, elongate; palmar tubercle somewhat larger, bifid; no accessory palmar tubercles; 2 to several flat ulnar tubercles; heel with 1–3 small tubercles; sole smooth; no definite lateral ridges or fringe on toes; inner metatarsal tubercle oval, outer tubercle much smaller, round; no tarsal fold; prominent outer tarsal tubercles in juveniles, weak to well-developed in adults.

COLORATION: Adult males olive-brown, pale brown, orange or yellowish orange above; often with peach or orange markings on side of head; posterior thigh surface gray with white mottling; venter yellow to bright chartreuse; adult females brown to gray brown above; posterior thigh surface dark, almost black with pale lavender mottling; venter purplish, except immaculate cream in juveniles.

NATURAL HISTORY: The only information is provided in Campbell's original description. *Eleutherodactylus aphanus* is an inhabitant of upland wet forest. The three largest females (35–44 mm SVL) contained yolked oviducal eggs 1.4–2.4 mm in diameter.

DISTRIBUTION: Eastern Guatemala (Depto. Izabal) in the premontane zone of the Montañas del Mico and adjacent part of the Sierra de las Minas, in a known elevational range of 591–786 m (fig. 9).

Fig. 8. Adult *Eleutherodactylus aphanus* Campbell, a light colored male and a darker female from Depto. Izabal, Guatemala. **Upper:** Male paratype (UTA-A 24480, 22 mm SVL). **Lower:** Female paratype (UTA-A 33414, 44 mm SVL). [Photographs courtesy of Jonathan A. Campbell.]

Eleutherodactylus biporcatus (W. Peters)

Figures 3B, 4–5, 10, 11 (map), 21E, F

Strabomantis biporcatus Peters, 1863: 405–407. Lectotype: Herewith designated ZMB 3330B, an adult female from "Veragua", in error for northern Venezuela.

Hylodes maussi Boettger, 1893: 39–40. Lectotype: SMF 3821 (not seen),[10] from Puerto Cabello, [Carabobo State], Venezuela, [near sea level; probably a general locality or shipping point as suggested by La Marca, 1992: 39]. NEW SYNONYMY.

Eleutherodactylus cornutus: Gines, 1959: 109 (fig.), 112.

Eleutherodactylus cornutus maussi: Rivero, 1961: 54.

Eleutherodactylus maussi: Lynch, 1975: 31.

DIAGNOSIS: This is the most distinctive of the species discussed here in having a coarsely areolate venter, a distinct inner tarsal fold, and vocal slits in adult males. None of these features is present in the other taxa covered in this review.

MORPHOLOGY: Adult males about 30–38 mm; adult females 49–74 mm (mean SVL = 36.1 mm, 6 ♂, 59.5 mm, 9 ♀); tibia 48–57% of SVL; head width 39–54% of SVL; cranial crests rather low, no raised bosses at posterior end of crests and no distinct otic crests; dorsum smooth to tuberculate (fig. 10) between major ridges and/or tubercle series; juveniles much more tuberculate than adults, often with short ridges of coalesced tubercles especially laterally; flanks tuberculate to granular; paired suprascapular plicae usually distinct, forming a chalice- or hourglass-shaped system, often connected or nearly connected by a medially directed arm from each plica; a completely separate pair of usually distinct)(-shaped or posteriorly diverging paravertebral plicae at midbody; a weak laterosacral ridge system of small tubercles or a few large, irregularly arranged black-tipped warts, absent in some individuals or occasionally lengthened posteriorly to form a V-shaped ridge system (e.g., AMNH 70547); venter coarsely areolate; snout truncate from above; nostrils not protuberant; snout short, slightly obtuse in profile; eye moderate, about equal to loreal distance (E-N); upper eyelid with many moderate-sized supraocular tubercles or only a few large ones; superciliary tubercles moderate-sized and widely spaced; eyelid width almost equal to IOD; tympanum large, equal to or larger than length of eye in males, three-fourths to equal in females; vomerine odontophores slightly arched, lying posterior and mediad to choanae; patches narrowly separated medially; subarticular tubercles rounded and projecting on all fingers; thenar tubercle raised, oblong; palmar tubercle larger, strongly bifid, outer segment oblong, much smaller than inner; definite large accessory palmar tubercles; ulnar tubercles evident in juveniles, weak or absent in adults; heel with scattered small tubercles; sole of foot with large plantar tubercles; weak keels on toes; inner metatarsal tubercle prominent, an elongate ovoid; outer metatarsal tubercle round, low; a well-developed inner tarsal fold.

COLORATION: Adult and juvenile *Eleutherodactylus biporcatus* are similar in dorsal coloration except that juveniles have more dark markings. Upper surface brown; plicae outlined by black, or dark pigment reduced to scattered spots; large tubercles in laterosacral area black, outlined by cream; dark bordered, light interorbital bar in some juveniles but not in large adults; upper lip uniform or usually barred with darker pigment on the brown ground color; lower margin of orbit usually marked by two or more black, light-edged spots; light supratympanic fold, usually bordered by black below; no black spot on tympanum; no complex black and white marking on the groin, which is similar in color to venter and flank; upper limb surfaces barred with darker pigment on brown ground color; bars much more evident in juveniles than in adults; posterior thigh surface dark brown with many tiny yellowish spots; dark seat patch around vent; no contrasting series of dark and light bars on inner surface

[10] Mertens (1967: 39) listed this specimen as holotype, which, in this case, probably qualifies as designation of lectotype "by inference" (Internatl. Commission., 1999: art. 74.6). As assumed by Mertens, Boettger (1893: 39–40) probably based his description on the single specimen presumed to be adult. But Boettger mentioned having two young specimens also. Such ambiguity as to whether or not "a nominal species-group taxon was established on a single specimen" is commonplace in the older literature, although the additional specimens nowadays are usually considered as syntypes ("cotypes" formerly). One of Boettger's juvenile specimens may have been exchanged to the Museum of Comparative Zoology as a "cotype" (specimen cited by Lynch, 1975: 42).

Fig. 9. Central America, showing distributions of *Eleutherodactylus aphanus* Campbell and *Eleutherodactylus megacephalus* (Cope).

of shank; edge of throat brown with numerous tiny cream spots; a series of light spots along edge of lower jaw in juveniles; venter light tan to whitish with numerous small whitish spots, one on each ventral areolation; undersides of limbs similar to throat in coloration.

NATURAL HISTORY: Heatwole (1962) gathered data on *Eleutherodactylus biporcatus* (then known as *E. cornutus maussi*) over a period of several months in the cloud forest or montane rain forest of Rancho Grande. He found that specimens were sedentary both in the field and in cages, remaining in the same spot for several days at a time and sometimes returning to the same site after once leaving it. The hiding and resting place of one specimen (presumed ♀ 50 mm SVL) "was under leaf litter and in a small cavity in the clay just large enough to accommodate . . . bottom of the cavity was covered with fragmented leaves". This frog was observed for nearly three weeks before it abandoned the site. Heatwole (1962: 5) cautioned that his observations might have reflected a tendency of the frogs "to return to the same place after

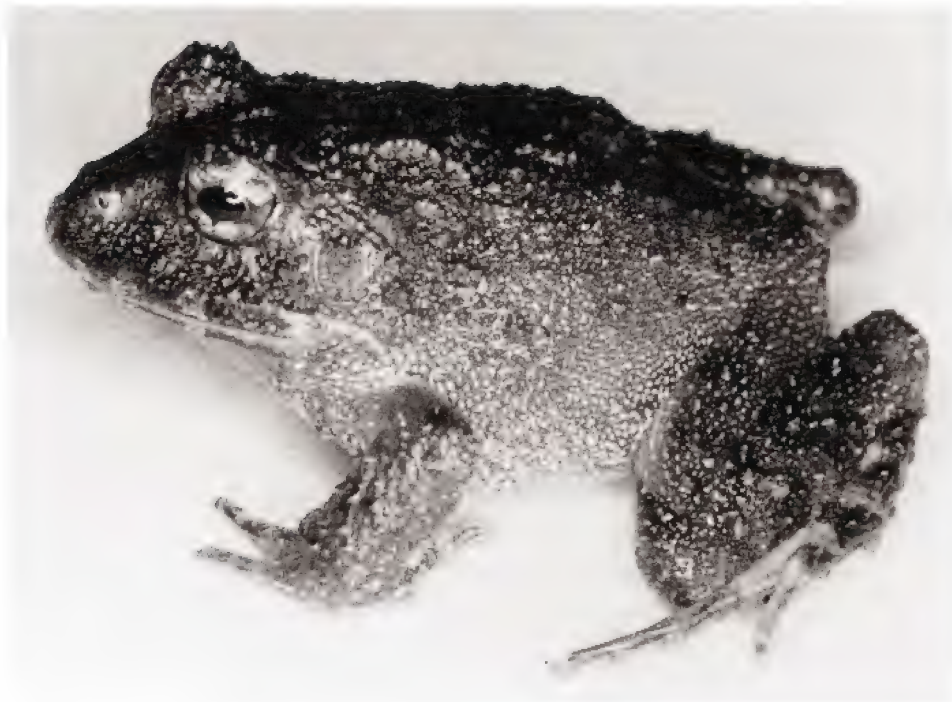

Fig. 10. *Eleutherodactylus biporcatus* (W. Peters). An unsexed subadult (KU 166369, 37 mm SVL) from Rancho Grande, Venezuela. [From a transparency by W. E. Duellman.]

activity periods rather than [strictly] sedentary habits as frogs forced to move often returned to their original location before the next observation period."

Based on examination of ovaries, Heatwole (1962: 2) thought that the species bred in both rainy and nonrainy seasons. He found a female of 60 mm SVL attending a clutch of 45 eggs in a cavity under leaf litter: "The cavity was just large enough to accommodate the eggs and female, and appeared to have been made by her . . . On top of her was a layer of litter 4 cm thick." Two of the eggs, measuring 4.4 and 8.4 mm, were unpigmented and contained advanced embryos with large yolk reserves; partial data were obtained on development and hatching. Newly hatched froglets averaged 10.7 mm SVL (10–11.4 mm, $N = 14$).

Heatwole discovered the aforesaid nest after tapping a pile of litter and eliciting a "screeching sound" from beneath (1962: 2). He went on (1962: 4) with comments on defense mechanisms and maternal care:

> [*Eleutherodactylus biporcatus*] has the responses to disturbances that are commonly encountered in other anurans such as inflating with air or voiding urine when captured. An additional behavioral pattern . . . deserves comment. When the litter was removed from above the female attending eggs, she inflated herself, raised up on all four legs, lowered her head and arched her back in a manner reminiscent of the defense–fight reaction of *Bufo* (Noble 1931). Whenever she was touched she emitted the startling shriek which had led to her discovery. Neither females not attending eggs nor males displayed this striking behavior pattern.

Males are not known to vocalize, although the presence of vocal slits is suggestive that they may (see also footnote 3). Courtship or amplexus has not been reported for the species. Heatwole (1962: 4) found specimens in the stomachs of two colubrid snakes (*Dendrophidion* and *Liophis*).

DISTRIBUTION: *Eleutherodactylus biporcatus* (s.s.) is endemic to northern Venezuela, where it seems to be known only from a few premontane localities in the Cordillera de la Costa and in the Serranía del Interior (fig. 11; earlier maps in Lynch [1975: 18] and La Marca [1992: 112], as *E. maussi*).

REMARKS: *Eleutherodactylus biporcatus*

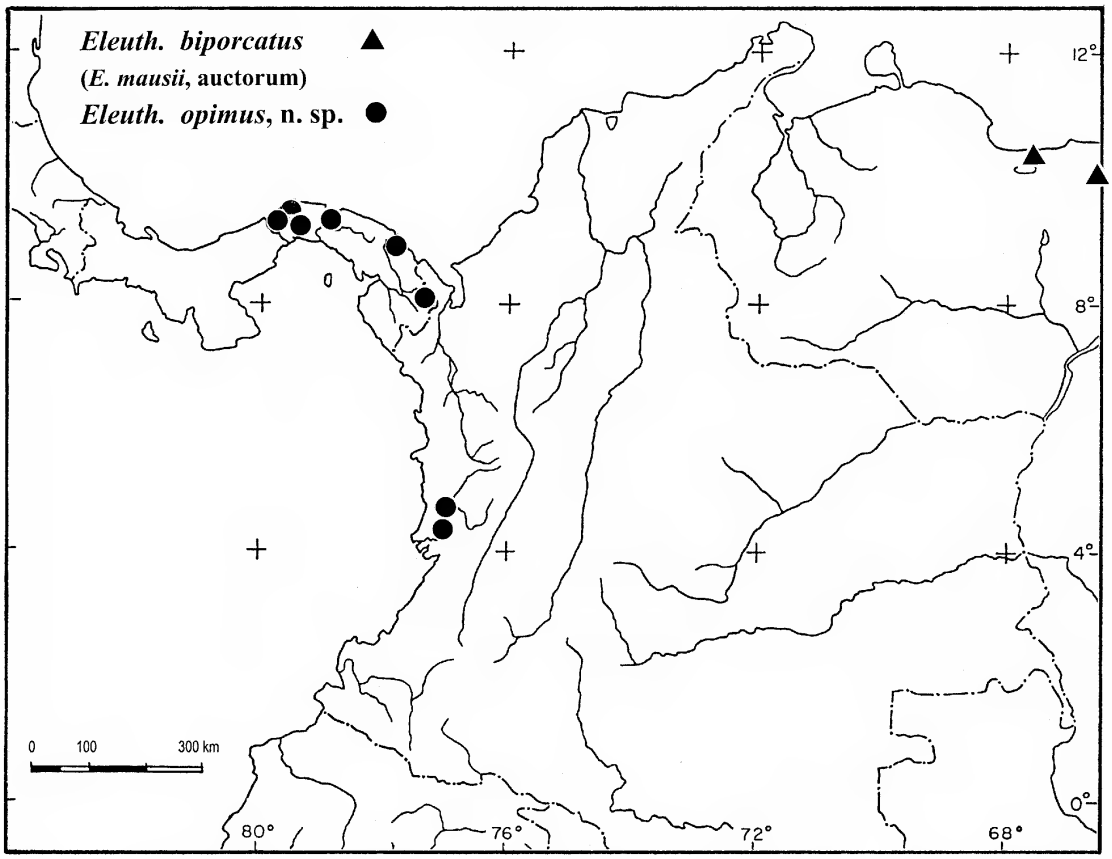

Fig. 11. Locality records for *Eleutherodactylus biporcatus* (W. Peters) in the Cordillera de la Costa and Serranía del Interior of northern Venezuela, and *Eleutherodactylus opimus*, new species, in eastern Panama and western Colombia.

(s.s.) is known mainly from the high wet forest at Rancho Grande (see Beebe and Crane, 1947) in the Cordillera de la Costa, but one available specimen extends the range over 100 km southeastward to the Serranía del Interior. This frog (KU 185672), a well-preserved adult female 63 mm SVL, was collected by Scott J. Maness on the night of February 10, 1974 from "rd → 1.5 K, Guzmanera trial [trail?], P[arque] N[acional] Guatopo, Miranda" (according to a list prepared by Maness for specimens sent to KU, courtesy of J. E. Simmons). It was collected at the same time as a specimen of *Bufo* "*typhonius*" (KU 185715); the elevation was not recorded and no other data are available. (Maness at that time was a Peace Corp Volunteer stationed at Rancho Grande; later, he and a companion were killed fighting a fire in Florida scrubland in 1981, while in the employ of the U.S. Fish and Wildlife Service.)

Heatwole (1962: 1–2) reported a maximum size of 30.2 mm SVL for a male in a preserved sample of 20 frogs (presumably 10 of each sex), and a maximum of 74 mm SVL in a field-encountered female (presumably released). He postulated that sexual maturity in females was attained at about 60 mm SVL "as no individuals smaller than this contained mature ova". Our small sample (table 2) indicates a larger size for males (to 38 mm) and a smaller size for sexually mature females.

Eleutherodactylus gulosus (Cope)

Figures 1, 3A, 12–13, 14 (map), 21A

Lithodytes gulosus Cope, 1875: 112–113. Holotype: USNM 32590, an adult female from "Spur of the Pico Blanco", Costa Rica, "at

Fig. 12. *Eleutherodactylus gulosus* (Cope). An adult female (AMNH 124370, 84 mm SVL) from continental divide above upper Quebrada de Arena, 1160–1220 m, Chiriquí, Panama. [From a transparency by C. W. Myers.]

6000 feet elevation", error for Cerro Utyum, Cantón de Talamanca, Provincia de Limón, Costa Rica, 1829 m (see Savage, 1970, 1974).
Hylodes gulosus: Boulenger, 1882: 211.
Eleutherodactylus gulosus: Noble, 1918: 330.
Eleutherodactylus rugosus (part): Taylor, 1952: 730.
Eleutherodactylus biporcatus (part): Lynch, 1975: 23. Jungfer. 1988: 15 (part [photograph = *E. megacephalus*]).

DIAGNOSIS: The smooth- or nearly smooth-skinned adults of this large species (fig. 12) are immediately distinguished from all other members of the group by the complete absence of dorsal ridging or plicae on the body, although distinctly shaped suprascapular plicae are faintly indicated in most juveniles (fig. 13), which have pustulate skin (figs. 1, 13). *Eleutherodactylus gulosus* further differs from its geographically closest relatives (*E. megacephalus, E. rugosus*) in having the black "seat patch" marking restricted to a small area immediately surrounding the vent, and in lacking conspicuous pale areas in a dark reticulum across the chest.

MORPHOLOGY: Adult males unknown (perhaps about 40–60 mm SVL?), adult females 72–103 mm; tibia 49–57% of SVL; head width 46–52% of SVL; frontoparietal crests well developed in larger specimens (but not posteriorly knobbed), and a definite palpable otic crest, terminating well above the supratympanic fold as an externally expressed

Fig. 13. *Eleutherodactylus gulosus* (Cope). Dorsal view of a juvenile (AMNH 124368, 19.7 mm SVL) showing characteristically configured anterior pair of short, weak suprascapular plicae (arrows), which disappear during ontogeny, ×4.8. The lateral edges of the plicae are emphasized by dark pigment. The transverse dark line between the posterior ends of the plicae conceals (in some specimens) a weak tubercular connecting ridge. The pustulate nature of the dorsal skin in juvenile *E. gulosus* is even more evident in life (see fig. 1).

boss in larger specimens; dorsal surfaces smooth or with scattered low tubercles in adults, but covered with many small pustules in juveniles; no suprascapular ridges in adults, but most juveniles in the range of 18–32 mm SVL usually with distinctly shaped but weakly developed anterior suprascapular plicae (fig. 13); no V-shaped or parallel ridges or rows of enlarged tubercles in laterosacral region of either adults or juveniles; flanks granular, with weak lateral ridges in a few specimens (AMNH 124371–124372); venter smooth; snout outline from above truncate; snout short, slightly obtuse in profile; nostrils not protuberant; eyes moderate, length about equal to loreal distance (E-N); upper eyelid with a few large tubercles mixed with many small pustules in juveniles, width less than IOD; tympanum relatively small, 35–52% of eye length in 10 juvenile males ($\bar{x}$ = 45.1%), 34–51% in 8 juvenile females ($\bar{x}$ = 39.8%), 42–54% in a subadult and two adult females ($\bar{x}$ = 49.7%); tympanum an anteriorly tipped vertical oval (appearing nearly round in one juvenile, AMNH 95042), tympanum length 71–94% of height ($\bar{x}$ = 81.6%, N = 21); vomerine odontophores triangular, lying posterior and mediad to choanae, patches narrowly separated medially; subarticular tubercles ovoid and flattened under fingers, ovoid and slightly projecting under toes; thenar tubercle large, elongate; palmar tubercle low, bifid to trifid; no definite accessory palmar tubercles; no ulnar tubercles; heel with 1 or 2 weakly enlarged tubercles; sole smooth; no definite lat-

eral ridge or fringe on toes; a prominent, large, oval inner metatarsal tubercle, outer tubercle low, much smaller; no tarsal fold; tarsus smooth.

COLORATION: Two adult females (72, 84 mm SVL) from Panama uniform dark brown above in life and in preservative; subadult female (46 mm SVL) orange-brown darkened by vague black mottling in life, lighter brown in preservative with some obscure black spots on posterior dorsum and dark bars on limbs; juveniles lighter brown—individually variable in life (blackish brown, brown, light orange-brown, or yellowish brown)—with dull darker brown spotting and mottling on back and darker brown bars on limbs; anterior dorsum of juveniles sometimes relatively free of dark pigment, showing as a light area between suprascapular plicae, which are edged in dark pigment, with a transverse dark line connecting the posterior ends of the plicae (fig. 13); usually a light interorbital bar bordered by brown posteriorly in juveniles; upper lip uniform to weakly barred with brown and tan in juveniles; uniform or with small light lip spots in adults; lower border of orbit marked with alternating small black and lighter spots in adults, much duller or absent in juveniles; supratympanic fold black in adults, colored similar to rest of head in juveniles; tympanum colored like rest of head in juveniles, uniform dark brown or with a black spot in adults.

No complex contrasting mark in the groin, which tends to be weakly and vaguely mottled brown on white (marbled blackish gray on white in a subadult female); in life, underside of head nearly uniform light brown or gray-brown in adult females, gray with small white spots and an irregular midgular light stripe in a subadult female; underside of upper arm, hind limbs, and venter mottled or spotted with brown on white in adults; throat and chest of juveniles greenish gray with white speckling on throat and white spots on chest; undersurfaces of limbs and posterior venter bright greenish yellow without markings in juveniles; posterior surface of thighs of adults nearly uniform silvery gray in life below obscure dorsal dark bars (dull light spots or short vertical dashes noted in preservative); posterior thigh of juveniles in life irregularly and inconspicuously mottled pale tan and black (tan and brown in preservative) below posterior extensions of the dark limb bands; "seat patch" small, comprising a discrete blackish mark immediately around vent or obscured by dorsal color in largest adults; tongue light yellow in an adult; inside lower lip light yellow and base of tongue yellowish white in juveniles; buccal cavity otherwise white; series of small light spots along lower lip margin except in large adult females; iris bronzy brown with dense fine black venation in adults, venation less evident in juveniles. Examined in good light, the iris for one series of juveniles (AMNH 95035–95046) was described in fieldnotes as

> bronze on upper half, turning (without sharp demarcation) slightly duller or paler bronze on lower half, and marked overall with dense, poorly defined black venation; a few individuals have the vaguest hint of a dark horizontal streak through the pupil.

NATURAL HISTORY: Except for descriptions of its habitat in Panama, very little is known about *Eleutherodactylus gulosus*. Juveniles were common at an elevation of 1000 m, on the forest floor by day at the Fortuna Dam site (in 1976 before construction of the dam had been started), at the narrow downstream end of the valley of the upper Río Chiriquí. Specimens later were found in the upper part of this humid highland valley at Quebrada de Arena and on the continental divide above the upper Quebrada de Arena. As mentioned under Remarks below, Myers and Duellman (1982: 12–14) described the geography of the highland valley of the upper Río Chiriquí. Myers et al. (1984: 13) described the habitat on the continental divide (> 1100 m) as a cool cloud forest that

> receives almost daily fog that is frequently accompanied by rain and mist. This cloud forest is a facies of high-canopied lower montane rain forest. Tree growth is very dense, and there is a frequently dense herbaceous and fern layer at ground level. There is a modest "moss layer" on the trunks of trees, which support a profusion of epiphytic growth, including bromeliads.

Except for one individual picked up at night, all specimens were on the surface of the leaf litter by day. The largest Panamanian female (fig. 12) was sitting placidly on the ground on a narrow ridge, next to a log

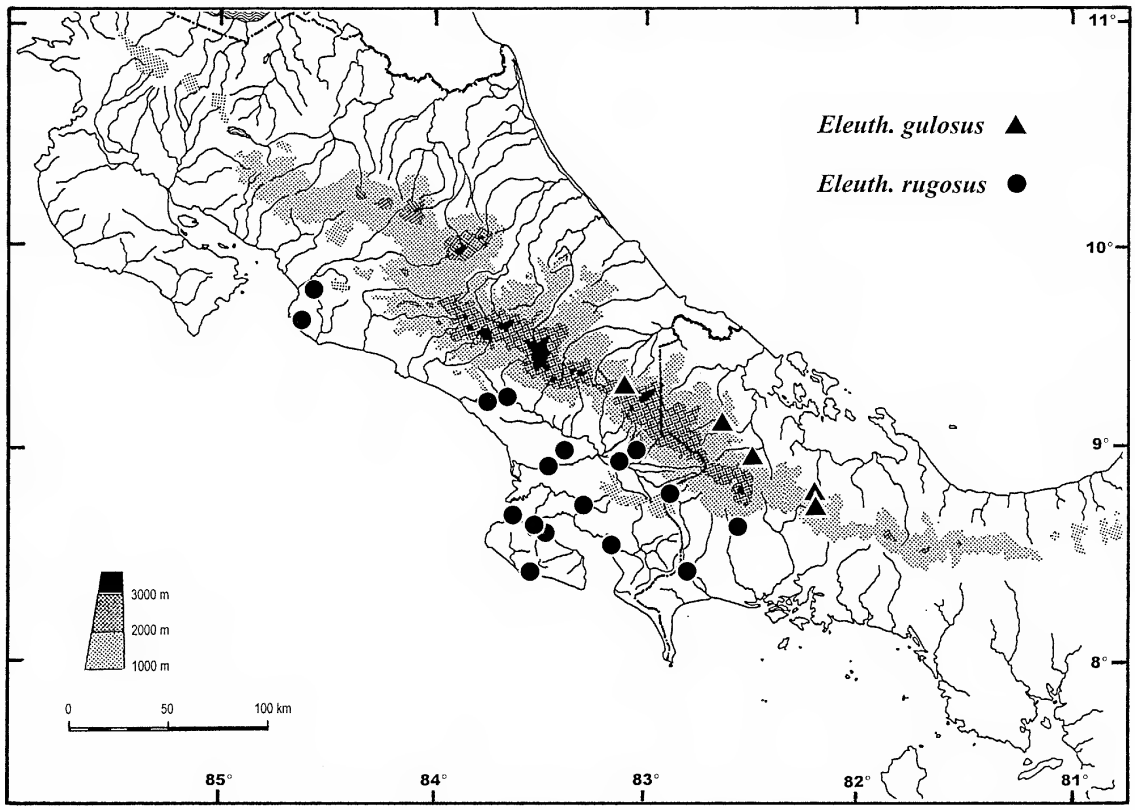

Fig. 14. Costa Rica and western Panama, showing localities for *Eleutherodactylus gulosus* (Cope) and *Eleutherodactylus rugosus* (W. Peters).

where the collector was having lunch. A few individuals were kept for a while in captivity at the American Museum, where they fed readily on crickets and appeared to be sit-and-wait predators. One adult female (72 mm SVL) also ate baby mice.

DISTRIBUTION: Humid premontane slopes of the Cordillera de Talamanca in southern Costa Rica and extreme western Panama, with an elevational range of 1000–1220 m, perhaps to 1830 m (fig. 14).

REMARKS: As pointed out by Myers and Duellman (1982), the area of the upper valley of the Río Chiriquí in Panama (where this species was rediscovered), although on the Pacific slope, has a strongly Atlantic-versant herpetofauna. This results from its location to the south of a low section of the continental divide, which dips below 1200 m above the upper Río Chiriquí Valley. Ascending air currents from the Atlantic versant spill into the valley before having lost most of their moisture orographically; this moist air funnels through the narrowing valley, profoundly affecting the climate and biota on this part of the Pacific versant. *Eleutherodactylus gulosus* is probably a primarily Atlantic-versant species as it is not known from the relatively well-collected Pacific slopes of Panama west of the Fortuna region.

The ontogenetic change in the dorsal integument is striking in this species. Juveniles are strongly pustulate (fig. 1) and have faint but usually discernible short, anteriorly situated suprascapular plicae (fig. 13), whereas the few adults available have essentially smooth dorsa (fig. 12). The subadult female (AMNH 124371, 46 mm SVL) retains fewer, less conspicuous pustules, and the suprascapular ridging has virtually disappeared. Adults have on each side a conspicuous otic knob or boss showing prominently behind the eye and above the tympanum (fig. 12). This knob—the external expression of the raised

terminus of the otic crest—is discernible in the larger juveniles, being positioned immediately under the suprascapular plica.

There also is ontogenetic change in dorsal coloration. Adults (fig. 12) become an overall darker color, and the rear of the thigh, which is indefinitely mottled or spotted with pale tan in juveniles, turns silvery gray in adults, the largest of which had also acquired silvery gray coloring along the lower sides and anterior face of the thigh. Dark barring on the hind limbs is evident in juveniles (fig. 13), obscure or obsolete in large specimens.

Ontogenetic change in ventral coloring is striking. Juveniles have the underside of the head and chest greenish gray, with white speckling on throat and with larger white spots on chest, with the greenish hue and chest spots disappearing in adults. The belly is conspicuously bright greenish yellow in juveniles, but white with brown mottling in adults.

We have accepted Cope's (1875) relatively fresh measurement of 103 mm for the *gulosus* holotype; during a brief examination, Myers jotted down "95 mm SVL" a century later; Lynch's (1975: 23) maximum size of "110 mm SVL" for female *E. biporcatus* s.l. was based on the same specimen (personal commun.). Even with the lesser figure, *Eleutherodactylus gulosus* attains the largest size in the *biporcatus* group. The largest females of *E. biporcatus* s.s. and *E. megacephalus* approach or slightly exceed the lower end of the size range of *E. gulosus* (table 2).

Eleutherodactylus megacephalus (Cope)

Figures 3D–E, 6, 9 (map), 15–16, 21B

Lithodytes megacephalus Cope, 1875: 110–111, pl. 23, figs. 5, 11, 11a. Holotype: USNM 32579, an adult female from "spur of the Pico Blanco", Costa Rica, "at 6,000 feet elevation" = Cerro Utyum, Cantón de Talamanca, Provincia de Limón, Costa Rica, 1829 m (see Savage, 1970, 1974).

Hylodes megacephalus: Brocchi, 1882: 57; Boulenger, 1882: 211.

Hylodes biporcatus (part): Boulenger, 1882: 220.

Eleutherodactylus rugosus: Noble, 1918: 329.

Eleutherodactylus biporcatus: Dunn, 1931: 410; Lynch, 1975: 23 (part). Jungfer, 1988: 16 (part [confused with *E. gulosus* specimens]).

DIAGNOSIS: Moderate-sized (males) to large (females) frogs (fig. 15) having well-developed suprascapular plicae and a definite laterosacral system of linearly arranged tubercles or tuberculate ridges, and with the dark seat patch mark continuing onto the thigh. Unlike the more rugose *Eleutherodactylus rugosus*, the posterior thigh surface in *E. megacephalus* is not contrastingly barred with black and red (white in small juveniles) but may be uniform or dark with some small yellow spots or mottling.

MORPHOLOGY: Adult males 30–43 mm SVL, adult females 50–70 mm (mean SVL = 33.6 mm, 10 ♂, 61.6 mm, 10 ♀); tibia 46–60% of SVL; head width 44–55% of SVL; large knobs or bosses at posterior end of cranial crests; distinct bony otic crests in large adults, with a terminal boss or knob externally evident above supratympanic fold in large females; dorsum smooth to tuberculate between major ridges and tubercle series; scattered pale-tipped, pointed pustules of juveniles change ontogenetically to fewer and lower pustules in adults; flanks tuberculate to granular; paired suprascapular plicae forming a definite chalice- or hourglass-shaped system; a discrete paired series of raised lateral and sacral tubercles, usually forming a V-shaped ridge system (fig. 3D) or (in Panama) a pair of nonconverging parallel ridges (fig. 3E); venter smooth; snout outline from above truncate; nostrils not protuberant; snout short, slightly obtuse in profile; eye moderate about equal to loreal distance (E-N); upper eyelid with moderate numbers of widely spaced supraocular and superciliary tubercles, width less than IOD; tympanum large, 80–90% of eye length in males, 40–50% in females; vomerine odontophores triangular, lying posterior and mediad to choanae; patches narrowly separated medially; subarticular tubercles ovoid under fingers I–II, obtuse, flattened under fingers III–IV; thenar tubercle low, oblong; palmar tubercle, larger, rounded, bifid; no definite accessory palmar tubercles; ulnar tubercles well developed in juveniles, weak or absent in adults; heel with 1 or 2 enlarged tubercles; sole smooth; no definite lateral keel or fringe on toes; a prominent oval, sometimes compressed inner metatarsal tubercle, outer low, much smaller; no tarsal fold; several promi-

Fig. 15. *Eleutherodactylus megacephalus* (Cope). An adult female from La Selva Biological Station, Heredia Prov., Costa Rica. [From a transparency by Robert Wayne Van Devender.]

nent outer tarsal tubercles in juveniles, weak in adults.

COLORATION: Adult and juvenile *Eleutherodactylus megacephalus* are similar in dorsal coloration, except that juveniles usually have a lighter ground color so that the dark markings are more sharply defined. Upper surfaces usually gray-tan to olive-brown, sometimes with a strong salmon cast,[11] but large females may be dark brown; plicae outlined by black; distinct, small supra-axillary and sacral black spots usually present in association with enlarged tubercles; vague light interorbital bar or spot usually present, demarcated anteriorly and posteriorly by areas slightly darker than dorsal ground color; upper lip with a dull light stripe, barred dark and light, or uniform; lower margin of orbit usually bordered by alternating series of small black and cream spots; supratympanic fold usually black; usually a black spot on tympanum; no complex black and white marking in groin, which is uniform or similar to adjacent posterior venter in pattern and color; upper limb surfaces uniform or usually marked with obscure dark bars; posterior thigh surface dark brown to black, uniform or variously spotted or mottled with light but never with vivid alternating black bars and red or white interspaces; black seat patch usually continuous with black background of lower posterior thigh which extends some distance onto undersurface of thigh; no contrasting pattern of black and white bars or white spots on inner surface of shank; throat variable, light with small brown punctations to mostly brown with small light spots or

[11] Jungfer (1988: 16) published a photograph of an apparently young male specimen (from Coclé Province, Panama) that reproduced as a vivid light orange.

covered with large light spots or a reticulum as on chest or venter; obscure, narrow light midgular stripe rarely present; series of light spots along edge of lower jaw in juveniles, lost in large adults; throat and chest covered anteriorly by a brown reticulum containing large round light spots in juveniles; reticulum and round spots covering most of venter in some examples but becoming irregular with increase in size; in some large adults, reticulum reduced to scattered dark spots; a similar pattern may be present on undersurface of thighs and shanks; Costa Rican juveniles have concealed yellow-orange to red-orange coloring[12] underneath the legs and in the light spots on the posterior venter, and on the palms of hands and underside of fingers and toes (sole of foot dark brown); anteriormost light ventral areas cream; with age, orange hues replaced by cream so adults usually have at most a little orange in groin and on digital tips; iris noted as black flecked with gold in Costa Rica.

The yellow-orange to red-orange ventral coloring in Costa Rican juveniles has not been noted by Myers in Panama.[13] His color notes on juvenile and subadult specimens from Panama (several localities in Bocas del Toro and one on north coast of Veraguas) recorded one tiny juvenile in which all ventral surfaces were bright greenish yellow. A greenish color under the hind legs was retained in some larger juveniles, but otherwise the throats were gray with white dots, and the venters were gray to black with white spots, or marbled in black and white. Rear thigh surfaces in Panama were variable: black with tan or yellowish tan spots, gray with white speckling, or silvery gray and black. The iris in Panama was described as brown or (usually) bronze, sometimes lighter below, with fine or dense black venation or with heavy black suffusion; one was greenish bronze with dense black venation.

NATURAL HISTORY: Nothing has been published on the breeding habits of *Eleutherodactylus megacephalus* and males are not known to call. The usual habitat is well-drained ground in tropical wet forest, including secondary growth and cacao plantations, but one was found in swamp forest near the Río Concepción on the north coast of Panama.

Juveniles are found active on the leaf litter both by day and night, although adults are seldom seen. Dunn (1931: 410, as *E. biporcatus*) noted the scarcity of adults on Barro Colorado Island in central Panama and hazarded a guess that they might "live in burrows". Based on a 13-month sampling program at La Selva in Costa Rica, Savage and his students (unpublished) concluded that adults are nocturnal and hide in burrows during the day, sitting at the burrow entrance at night and ambushing passing prey. Presumably they use burrows made by other animals inasmuch as frogs of this group are not known as excavators.

Noble (1918: 330–331, as *E. rugosus*) examined a few stomachs of Nicaraguan *Eleutherodactylus megacephalus* and found mostly beetles and a large ant (*Neoponera*). Lieberman (1986: tables 7–10, as *E. biporcatus*) reported a wide variety of arthropods and a "vertebrate" (presumably a frog or small squamate reptile) from 21 stomachs of frogs from La Selva, Costa Rica; the most important prey items by proportion of stomachs were beetles (30%), ants (23%), orthopterans (14%), isopods (9%), unidentified larvae (9%), and spiders (5%).

DISTRIBUTION: *Eleutherodactylus megacephalus* inhabits lowlands and premontane slopes on the Atlantic versant from southwestern Honduras to central Panama (fig. 9), where it also occurs in uplands on the Pacific versant. It is found from near sea level to 1200 m elevation, perhaps rarely higher (as already noted under Application of the Name *Lithodytes megacephalus*, the stated type locality at 6000 ft [1829 m] is unaccountably high).

REMARKS: As stated earlier (under Application of the Name *Lithodytes megacephalus* Cope, 1875), we have had to conclude that

[12] The bright juvenile colors in Costa Rica tend toward yellow in the smallest frogs of about 10–15 mm SVL, but are bright salmon to red-orange and most extensive in juveniles of about 25–30 mm SVL.

[13] However, in their very useful survey of the amphibians of the Panama Canal region, Ibáñez et al. (1999: 41, 139) state that the venter, groin, and concealed surfaces of the hind legs are *pale orange* or yellow in juvenile "*biporcatus*." The species referred to is uncertain, inasmuch as both *E. megacephalus* and *E. opimus* occur in the area of their study.

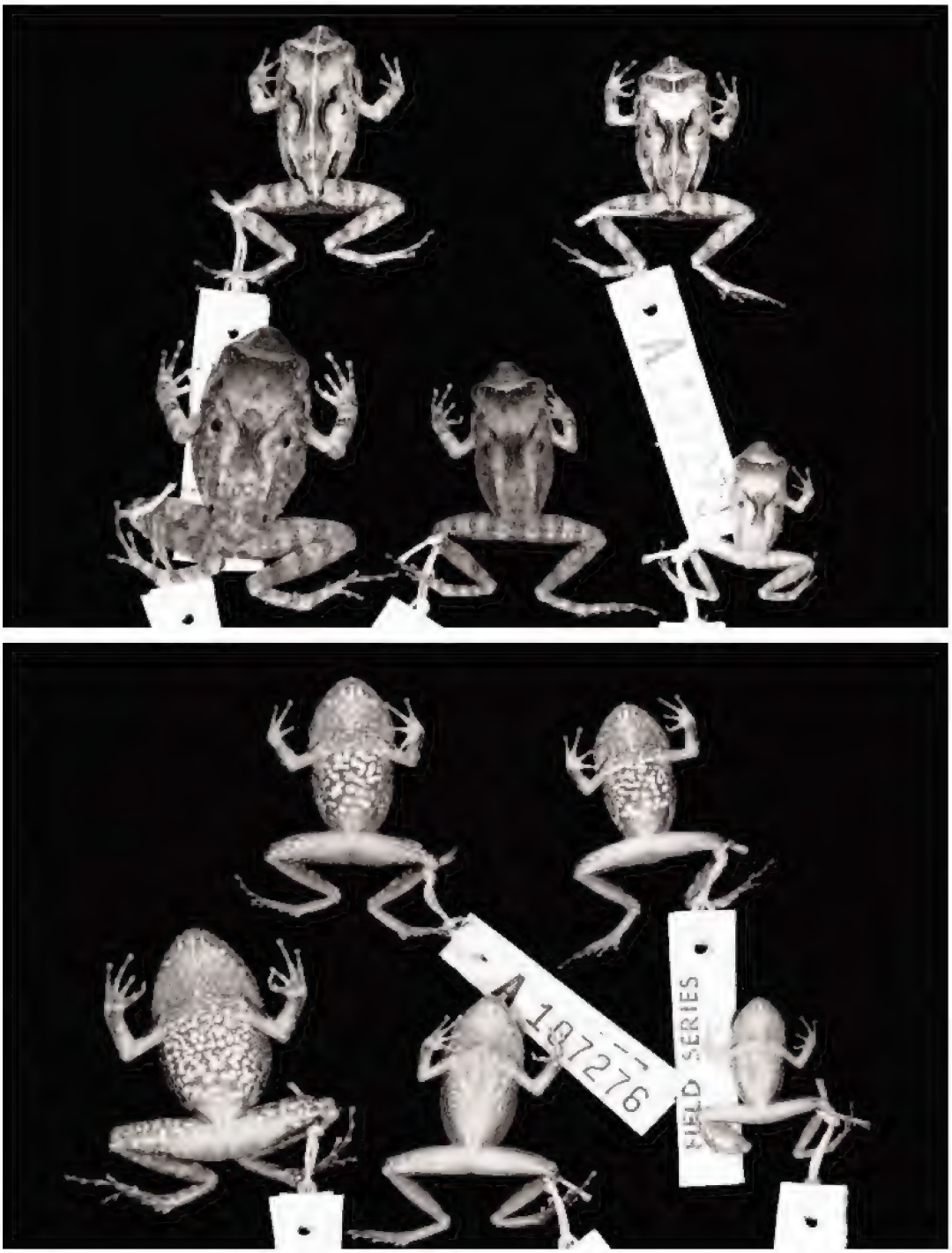

Fig. 16. *Eleutherodactylus megacephalus* (Cope), juveniles (×1.5) showing variation in the laterosacral ridge system—an instance of unusual intrapopulational variation, or of sympatry with an unnamed sibling species? Upper specimens left to right, AMNH 107276, 107279; lower specimens AMNH 107277, 107278, 107280; all from Quebrada El Guabo, 150–250 m, Bocas del Toro, Panama. The two uppermost frogs have posteriorly converging laterosacral plicae that meet in a V-shape, as is characteristic of Costa Rican populations of *E. megacephalus*. The three specimens in the lower row have a pair

Cope's holotype of *megacephalus* probably was collected at a lower elevation than stated and that, in any case, it almost certainly is conspecific with some lowland populations of frogs from the Atlantic versant of lower Central America. Following Dunn's Barro Colorado Island paper (1931), authors have erroneously assigned the name *Eleutherodactylus biporcatus* to lowland broad-headed frogs from Honduras to northwestern Colombia. But, in this sense, the misapplied name "*biporcatus*" proves to be a composite of at least three species, one of which (*rugosus*) is resurrected and another (*opimus*) is described as new on following pages.

The remaining part of the old "*biporcatus*" is here assigned to Cope's *Eleutherodactylus megacephalus*, with a distribution on the Atlantic versant from northwestern Honduras to central Panama, where there are some occurrences on the Pacific side of the low continental divide. However, even with this geographic restriction, there remains a concern that we may still be dealing with a composite species. This concern rises (1) from the conspicuous red or orange ventral coloring that is present in Costa Rican juveniles but lacking in Panamanian specimens (see last paragraph under Coloration above), and (2) from variation in the laterosacral tubercle or ridge system in populations in lowland Bocas del Toro in extreme northwestern Panama.

Concerning the laterosacral ridge system, the most relevant material available at this time (see fig. 16), is a small series from the foothills of the Cordillera de Talamanca in Atlantic-western Panama (AMNH 107276–107282, Quebrada El Guabo, 150–250 m, Río Changuinola drainage). Included are an adult female (54 mm SVL) and a subadult female (30 mm), both with V-shaped laterosacral ridges. Of five juveniles (fig. 16) in the series, two have the V-shaped ridges and three have nonconverging, parallel laterosacral ridges; they differ also in vividness of color pattern. None of the juveniles had red or orange ventral coloring. The smallest froglet (12.5 mm SVL) in figure 16 had all ventral surfaces uniformly bright greenish yellow except for scattered white spots on the chest; the other juveniles had the throat gray with irregular white dots, the venter patterned with larger white spots, and the rear of belly and undersides of the hind legs greenish flesh. The five juveniles shown in figure 16 are readily separated by laterosacral ridges and vividness of dorsal pattern into two kinds of frogs—but we are unable to conclude whether this is an instance of sympatric "sibling" species or one of intrapopulational polymorphism.

Therefore, we are not prepared at this time to give a definitive opinion on the status of frogs from the western half of the Isthmus of Panama, being hindered by the paucity of adult specimens and especially by the loss or temporary misplacement of several dozen critical specimens in the University of Kansas collections (see comment on page 43, Specimens Examined). Consequently, our assignment of Panamanian specimens to *E. megacephalus* is tentative.

Most Panamanian specimens assigned to *Eleutherodactylus megacephalus* are from the lowlands and intermediate elevations of Bocas del Toro Province. Other material examined by us is scattered and sparse. Myers collected a single juvenile (KU 113676) from the mouth of the Río Concepción, on the north coast of Veraguas Province, Panama, about halfway between Bocas del Toro and the Panama Canal at Barro Colorado Island, which is our easternmost record for *megacephalus*. Between those localities, we know *E. megacephalus* from the low continental divide north of El Copé (Coclé Prov.), at El Valle de Antón (Coclé), and at Cerro Campana (Panamá). Available specimens from these sites are all small juveniles or subadults. They agree with similar-sized *megacephalus* from Costa Rica in having the dor-

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of nonconverging, parallel plicae, which is the typical situation in Panamanian frogs currently assigned to this species. (The pale vertebral line in two frogs, although infrequent in the *biporcatus* group, is a common morph in many species of *Eleutherodactylus* and various other anurans; it probably lacks taxonomic significance.)

sum covered with widely-spaced whitish-tipped tubercles and evident suprascapular and laterosacral tubercle or ridge systems. (It will be recalled that during ontogeny in *E. megacephalus*, the tubercles not involved in the ridging system become reduced so that adults have a shagreened to nearly smooth dorsum, except for the suprascapular and laterosacral ridges.)

Frogs of this species group east of the Panama Canal differ most conspicuously from *Eleutherodactylus megacephalus* in lacking the laterosacral series of linearly arranged tubercles or ridges, as described in the next species account.

Eleutherodactylus opimus, new species

Figures 11 (map), 17–18, 21C

Eleutherodactylus biporcatus (part): Dunn, 1931: 410; Lynch, 1975: 23; 1997: 354, fig. 1 top (skull). Ruiz-Carranza et al., 1996: 395.
Eleutherodactylus biporcatus: Lynch, 1998: 145.

HOLOTYPE: AMNH 87020 (field no. CWM 10307), a subadult female from Quebrada Docordó, about 10 km above junction with Río San Juan, about 100 m elev., Depto. Chocó, Colombia (approx. 4°34′N, 77°03′ W), collected February 5–6, 1971, by C. W. Myers and John Daly.

PARATYPES: Colombia: *Chocó:* AMNH 109473–109487, AMNH 109471–109472. Panama: *Colón:* AMNH 89465, KU 108430–108431, 113677–113678, 172226–172228. *Darién:* KU 76221, 76226. *Panamá:* AMNH 53704, 89464, KU 80326, 108432–108433, 108434–108435. *San Blas:* KU 113679. The species description is based primarily on the holotype and the specimens designated as paratypes. See the appendix (Specimens Examined) for complete locality data for paratypes.

REFERRED SPECIMENS: See also Specimens Examined for additional material assigned to *E. opimus* (specimens not at hand when the final description was written). Specimens indicated by "***?**" were lost or misplaced before we could confirm identification and therefore can only tentatively be assigned to *E. opimus*, although that assignment for KU 108934 is questionable (see footnote 15).

ETYMOLOGY: The species name *opimus* is a Latin adjective meaning rich or fruitful and also, as in the present context, well-fed or fat.

DIAGNOSIS: Moderate-sized (males) to large (females) frogs (fig. 17) resembling *E. megacephalus* in having well-developed suprascapular plicae and sometimes a white-spotted venter, but differing in lacking a definite laterosacral system of paired linear or V-shaped tubercles or ridges (fig. 18). *Eleutherodactylus opimus* is readily distinguished from Costa Rican *E. rugosus* in being much less tuberculate and in color pattern (*rugosus* with posterior thigh brightly barred black and red, and often with dorsolateral stripes). Superficially, *E. opimus* resembles the smaller Guatemalan *E. aphanus*, which differs in having an immaculate venter lacking any indication of dark markings or white spots; *opimus* also lacks the weak finger and toe keels of *aphanus* (Campbell, 1994: 298).

MEASUREMENTS OF HOLOTYPE (in mm): The holotype is a subadult female having tiny ova (to about 0.3 mm) and thin (0.2) nonconvoluted oviducts. SVL 41.9, tibia length 21.5, foot length from proximal edge inner metatarsal tubercle to tip of toe IV 18.5, head width 20.5, head length on the diagonal from angle of jaw to tip of snout 17.2, upper eyelid width 4.9, interorbital distance 4.7, eye to posterior edge of nostril 5.0, eye length 5.6, tympanum length 2.9.

MORPHOLOGY: Size of adult males unknown (perhaps about 30–40 mm SVL?), one adult female 69 mm SVL; tibia 49–56% of SVL (3 subadult and adult ♀); head width 43–50% of SVL; cranial crests present (absent in smaller juveniles), posteriorly raised or bossed in adult female; bony otic crest evident in larger specimens, terminating in an externally expressed boss or knob; dorsum weakly to pronouncedly pustulate between major ridges and in sacral region, with scattered small tubercle; flanks tuberculate to granular; paired suprascapular ridges forming a definite chalice- or hourglass-shaped system; no discrete enlarged lateral and sacral tubercles or ridges forming either a parallel paired or V-shaped laterosacral system; most specimens with 2–4 widely spaced posterior sacral tubercles forming a transverse series; smallest juveniles sometimes with several small sacral tubercles aligned on each

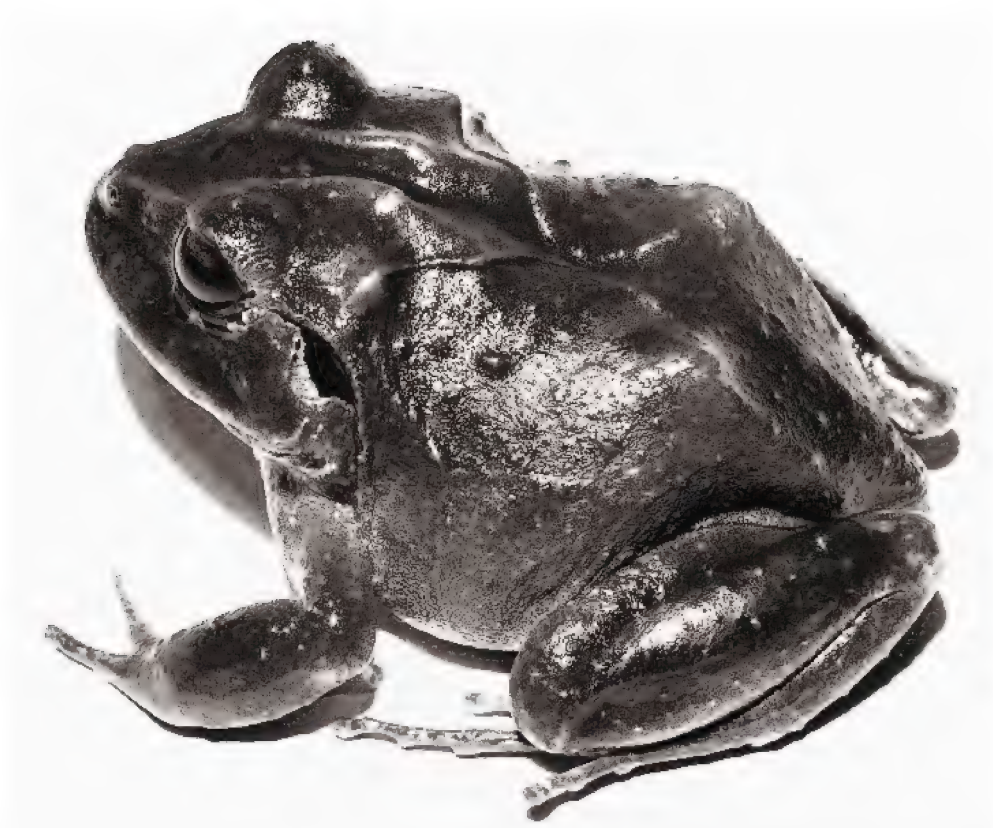

Fig. 17. *Eleutherodactylus opimus*, new species. An adult female from Camp Summit, 300–400 m elev., San Blas-Darién border, eastern Panama (KU 113679, 69 mm SVL). [Photograph by C. W. Myers.]

side in a discontinuous longitudinal series in anterior sacral region, these being ontogenetically lost or reduced to a few widely spaced tubercles; venter smooth; snout short, its outline truncate from above, slightly obtuse in profile; nostrils not protuberant; eye moderate, roughly equal to distance from its anterior edge to nostril; upper eyelid including supraciliary margin pustulate and tuberculate, with tubercles subequal or with several supraocular tubercles larger than others; eyelid width more or less equal to interorbital distance; tympanum large, roughly half of eye length in females, larger in males; vomerine odontophores triangular, lying posterior and mediad to choanae, the patches narrowly separated medially; subarticular tubercles ovoid and slightly protuberant under all fingers or barely flattened under III–IV; thenar tubercle low, oblong; palmar tubercle nearly the same size, bifid; no definite accessory palmar tubercles except sometimes for one between the large palmar tubercle and base of finger IV; ulnar tubercles low and inconspicuous; heel with scattered small tubercles, none markedly enlarged; sole smooth; no definite lateral keel or fringe on toes; a prominent elongate, ovoidal inner metatarsal tubercle, outer tubercle much lower and smaller; no tarsal fold; outer tarsal tubercles weak or absent.

COLORATION: Small specimens of *Eleutherodactylus opimus* are often lighter than larger ones, with more evident dark markings, and there may be a tendency for general darkening during ontogeny—the largest specimen (fig. 17), an adult female, was almost uniformly dark brown with a silvery suffusion over the flanks and thighs. However, there is considerable variation in coloration, and even equivalent-sized specimens

Fig. 18. *Eleutherodactylus opimus*, new species. A juvenile showing presence of well-defined suprascapular plicae and absence of laterosacral plicae, ×2.4. (KU 113677, 25 mm SVL, from ridge about 4 km SE Puerto Pilón, 190–240 m, Colón Prov., Panama.)

may differ greatly in the intensity of the ground color (fig. 19).

Dorsal colorations in life include light to very dark shades of brown, including grayish, orangish, and reddish brown; plicae usually outlined by black; light-colored supraaxillary and sacral tubercles usually set in black spots; interorbital light bar present or absent, when present usually vague and demarcated anteriorly and posteriorly by areas slightly darker than dorsal ground color; margin of upper lip pale, broken by two usually conspicuous dark bars radiating from eye to lip, and sometimes with vague dark blotching anteriorly on lip; lower margin of orbit usually bordered by alternating small cream and black spots; the latter often superimposed on the two radiating dark bars; usually a black spot on upper side of tympanum, confluent with black edging on supratympanic fold; groin pattern variable, from uniformly pale to mottled black and white; upper limb surfaces variable, from virtually uniform to black barred; anterior thigh surface barred or not; lower side of posterior thigh blackish (in life black, dark brown, or black with areas of gray or silvery gray), confluent with the dark seat patch; throat varying from light (white in life) with suffusion or punctations of light brown, to medium or dark brown with small white spots, usually with an ill-defined white midgular stripe; a series of light spots along edge of lower jaw at least in small specimens. Small to large white spots in brown reticulum across chest, this pattern tending to extend ventrolaterally, leaving belly nearly immaculate white. Iris in life described as bronzy brown in Colombian holotype; varying in Panamanian specimens from bronze darkened by brown or black suffusion, to black with bronze flecking.

NATURAL HISTORY: Nothing is known of breeding habits. The usual habitat is hilly or well-drained areas in tropical wet forest. Myers found specimens (including the holotype) mostly on leaf litter by day, but three specimens from his "Camp Summit" locality, including a large female (fig. 17), were found on the forest floor by night.

Toft (1981: 141) found ants, orthropterans, and miscellaneous arthropod remains in three stomachs of *Eleutherodactylus opimus* (reported as *E. biporcatus*). Toft concluded in summary that most (8 of 9 spp.) of the leaf-litter *Eleutherodactylus* in her sample "are cryptic, sit-and-wait foragers which eat few large prey per day" (Toft, 1981: 139); *E. opimus* was included in this category by implication.

DISTRIBUTION: Lowlands and premontane areas from central Panama (east of Panama Canal) to northwestern Colombia on the Pacific versant (fig. 11).

REMARKS: *Eleutherodactylus opimus* differs from other members of the *biporcatus* group in having a distinctive karyotype, as based on preparations made by Dr. Shyh-Hwang Chen from three Panamanian specimens collected at Nusagandi (fig. 21C, and Chen, 2001).

As in the case of *Eleutherodactylus megacephalus*, available specimens of *E. opimus* consist mainly of juvenile and subadult frogs. We have seen no adult males and only one adult female (shown in fig. 17), which was collected by Myers at "Camp Summit" on the low continental divide between San

Fig. 19. Light and dark variants of *Eleutherodactylus opimus*, new species, in life. Both are subadult females of equivalent size (42–43 mm SVL) and with uniformly small ovarian ova. **Upper:** AMNH 87020 (holotype) from Quebrada Docordó in western Colombia. **Lower:** AMNH 89464 from El Llano-Cartí Road in central Panama. [Photographs by C. W. Myers.]

Fig. 20. *Eleutherodactylus rugosus* (W. Peters). An adult male from vicinity of Rincón de Osa, Puntarenas Prov., Costa Rica. [From a transparency by Roy W. McDiarmid.]

Blas and Darién in eastern Panama (locality discussed in Myers, 1969: 26). This individual (identified in the field as "*E. biporcatus*?") would have been designated as holotype, except that the skull (not seen) was removed before our reexamination of the specimen, and four other specimens (KU 113680–113681, 113693–113694) collected at the same locality were lost or misplaced before their identity could be confirmed. A lateral outline view of the skull was given by Lynch (1997: fig. 1 top) as *E. biporcatus*.

Eleutherodactylus rugosus (W. Peters)

Figures 3C, 7, 14 (map), 20, 21D

Hylodes rugosus W. Peters, 1873: 610–611. Holotype: ZMB 7812, a juvenile from "Chiriqui" = Provincia de Chiriquí, Panama.

Lithodytes pelviculus Cope, 1877: 89. Holotype: USNM 32326, west coast of Central America.

Lithodytes florulentus Cope, 1893: 336–337. Holotype: No. 327 G. K. Cherrie collection (now lost) from Boruca, Cantón de Buenos Aires, Provincia de Puntarenas, Costa Rica.

Hylodes florulentus: Günther, 1900 (1885–1902): 234.

Eleutherodactylus rugosus: Taylor, 1952: 730.

Eleutherodactylus florulentus: Taylor, 1952: 765.

Eleutherodactylus biporcatus (part): Lynch, 1975.

DIAGNOSIS: An extremely rugose, moderate-sized frog (fig. 20) trenchantly distinguished from *Eleutherodactylus megacephalus* and from all other species of the *biporcatus* group in having (except in smallest juveniles) black vertical bars alternating with scarlet interspaces on the posterior thigh surface, and contrasting light (usually red) and black markings in the groin and under surfaces of the hind limbs.

MORPHOLOGY: Adult males 27–44 mm SVL, adult females 35–65 mm (mean SVL = 36.1 mm, 10 ♂, 50.9 mm, 10 ♀); tibia 47–57% of SVL; head width 41–51% of SVL; large bosses or knobs externally expressed at posterior ends of frontoparietal crests and at terminus of otic crest above supratympanic fold in large adults; dorsum strongly tuberculate, with numerous large warts and ridges, and with many smooth to pointed tubercles that are sometimes white tipped; a chalice- or hourglass-shaped system of suprascapular plicae, often with a medially directed branch from each plica;

flanks tuberculate; venter smooth; snout short, slightly obtuse in profile; nostrils not protuberant; upper eyelid with numerous warts, several enlarged, width less than IOD; tympanum large, 80–90% of eye length in males, 40–50% in females; vomerine odontophores triangular, lying posterior and mediad to large choanae; patches narrowly separated medially; subarticular tubercles ovoid, obtuse under fingers I–II, flattened under fingers III–IV, slightly projecting under toes; ulnar tubercles well developed; thenar tubercle low, oblong; palmar tubercle larger, bifid; no definite accessory palmar tubercles; heel with 1 or 2 enlarged pointed tubercles; sole smooth; no definite lateral ridge or fringe on toes; an inner enlarged, oval metatarsal tubercle, outer tubercle much smaller, round; no tarsal fold; several prominent outer tarsal tubercles in juveniles, weak to well developed in adults.

COLORATION: Adult and juvenile *Eleutherodactylus rugosus* are similar in dorsal coloration except that juveniles are lighter and have the dark markings more vivid. Upper surfaces various shades of brown, but usually dark reddish brown with a pair of lighter (tan to reddish brown) broad dorsal stripes extending posteriorly from shoulders for about three-fourths of distance to groin; plicae and enlarged supra-axillary tubercles bordered by black; usually a light interorbital bar bordered by black posteriorly; upper lip barred black and tan to dull cream or no obvious pattern; lower margin of orbit often bordered by alternating series of small black and cream spots; supratympanic fold usually black; usually a black spot on tympanum; groin with white and black complex marking that is continuous with similar pattern on anterior and usually underside of thigh; arms obscurely barred with black above; hind limbs brown, barred with black on upper surfaces; black bars continue onto posterior thigh surface and are separated by bright scarlet interspaces; black lower third of posterior thigh surface and seat patch continuous; inner and often ventral surface of shank barred like posterior thigh or marked with large white spots on a dark brown field; throat suffused by dark brown pigment that may enclose tiny light spots; a narrow irregular midgular light stripe usually indicated; series of light spots along edge of lower jaw; chest and anterior venter or entire venter brown with large light spots; a similar pattern may be present on undersurfaces of thigh and shank; sole of foot dark; in juveniles, palms, toes posterior venter, undersurfaces of hind limbs bright orange to red; contrastingly marked light spaces on posterior thigh may be white in smallest examples.

NATURAL HISTORY: On the Osa Peninsula, Roy McDiarmid (unpubl.) observed that juveniles of *Eleutherodactylus rugosus* were diurnal and adults nocturnal. Adults were found in shallow depressions in leaf litter. The diet was primarily insectivorous, primarily coleopterans, but lizards and other frogs were occasionally eaten.

DISTRIBUTION: Lowlands and premontane slopes of the Pacific versant from the Río Carara, Puntarenas Province, Costa Rica (9°47′N) to extreme western Panama (10–1220 m; fig. 14).

REMARKS: Small juveniles of *Eleutherodactylus rugosus* are covered dorsally by large, scattered white-tipped tubercles. During ontogeny, the tubercles become darkened and tend to fuse into ridges. Adults retain tubercles and ridges to a much greater extent than in other species of the group. Most individuals of all ages have a pair of relatively broad, light tan to reddish brown dorsolateral stripes lateral to the suprascapular plicae and extending farther posteriad. The dorsolateral stripes are prominent in the holotype of this species, but do not occur in the variation of any other member of the *biporcatus* group.

Taylor (1952, 1954) anticipated our conclusion that this form is a valid species, although he applied the name *Eleutherodactylus florulentus* to it. He incorrectly used the name *Eleutherodactylus rugosus* for the populations recognized as *E. megacephalus* in the present paper. Although the main portion of the range of this species is around the Golfo Dulce, it also occurs a considerable distance northwestward along the lowlands of the Pacific coast, and into the inland El General and Coto Brus Valleys of Costa Rica.

IS THE *ELEUTHERODACTYLUS BIPORCATUS* GROUP MONOPHYLETIC?

That frogs of this group are unusual within the genus in having broad heads and cranial crests and lacking expanded digital disks was early recognized by Peters (1863), who erected a new genus (*Strabomantis*) for its first discovered member. The taxonomic history of the group is reviewed earlier in the present paper, where it is pointed out that Venezuelan *Eleutherodactylus biporcatus* sensu stricto and its allies belong to the Middle American clade (subgenus *Craugaster*) characterized by the E condition of the adductor mandibulae muscle. Most South American forms of *Eleutherodactylus*, including the broad-headed members of the *E. sulcatus* group have the S condition of the adductor.

Based on Bogart (1973, 1981) and DeWeese (1976), Savage (1987) pointed out that members of the Middle American clade, including *Eleutherodactylus rugosus* ("*biporcatus*"), were characterized by a 2N karyotype of 18, 20, or 22 chromosomes equal to a *nombre fundamental* (N.F.) of 36, 38, or 44. Much greater variation was found in those species having the S condition of the adductor mandibulae, but most South American forms have high 2N (32, 34, 36) and N.F. values (32, 36, 38, 44, 46). However, *Eleutherodactylus sulcatus*, a broad-headed Amazonian species (S condition), has a low 2N = 22, with N.F. = 38 (DeWeese, personal commun.).

DeWeese's (1976) examination of the karyotypes of *Eleutherodactylus rugosus* (reported as *E. biporcatus*) showed a 2N = 20 and N.F. = 38. Shyh-Hwang Chen of Taiwan Normal National University has recently completed a review of chromosome morphology in the Central American clade (*Craugaster*). His studies showed that *Eleutherodactylus gulosus* has a karyotype similar to that of *E. rugosus. Eleutherodactylus megacephalus* and *E. opimus* have similar karyotypes, with 2N = 20, N.F. = 36. Although differing in details of chromosome morphology, the similarities in karyotypes among these four species within the Central American clade seemed to confirm the recognition of the *biporcatus* group.

Then, Dr. Chen called our attention to a paper by Schmid et al. (1992) describing the karyology of *Eleutherodactylus biporcatus* (reported as *E. maussi*). In that study, 70 females and one male were reported to have a 2N = 36 (considered as the ancestral condition), whereas 15 additional males had 2N = 35. N.F.s for these karyotypes are 42.

Dr. Chen very graciously prepared idiograms of the karyotypes of members of the *biporcatus* group for us (fig. 21). The differences in morphology are striking and leave open to question whether there is a close relationship between the Central American species and Venezuelan *E. biporcatus* s.s. *Eleutherodactylus gulosus*, *E. megacephalus*, and *E. opimus* have karyotypes similar to that of *E. rugosus*. But the karyotype of *Eleutherodactylus biporcatus* is much more similar to those of species having the S condition of the adductor (e.g., *E. ridens*, 2N = 34, N.F. = 36) than to any other species of *Eleutherodactylus* having the E condition.[14]

The possibility then occurred to us that Lynch (1986) might have been mistaken in reporting the E condition in *Eleutherodactylus biporcatus* (as *E. maussi*). But dissection of specimens of this species (AMNH 70545, 70556) confirmed Lynch's observations that the E condition characterizes this taxon. We also have confirmed that the E state of the adductor is found in all other species assigned to the *biporcatus* group in this paper as previously noted by Lynch (1986) and Savage (1987) and including *Eleutherodactylus gulosus* (AMNH 95037).

Contrary to Miyamoto and Tennant (1984) and Lynch (1986), we regard both the E and S states of the adductor muscles as derived from the plesiomorphic condition where both the posterior subexternus and externus super-

[14] Added in press: Dr. Chen is now inclined to believe that the frogs used by Schmid et al. (1992) for karyotypic study may have been another species somehow misidentified as *Eleutherodactylus maussi* (*E. biporcatus* s.s.). Eight other named species of *Eleutherodactylus* occur in the Cordillera de la Costa (Lynch and La Marca, 1993: 144); all except *biporcatus* are known or thought to have the S condition of the adductor (based on the subgeneric assignments in Lynch and Duellman, 1997: 219–234). Because there are no preserved voucher specimens (Schmid, personal commun.), we could not verify the identification of the species studied by Schmid et al., whose work needs corroboration.

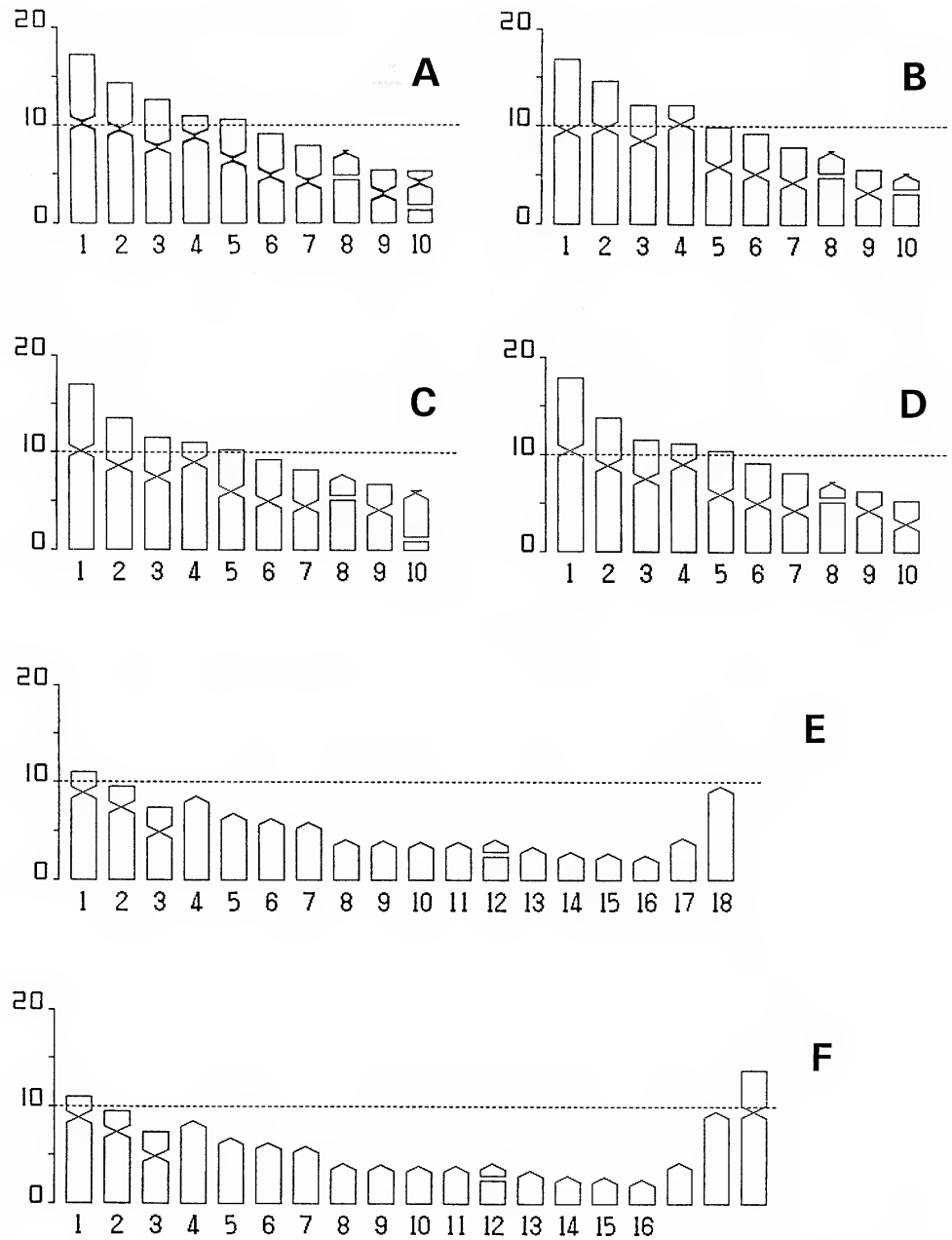

Fig. 21. Idiograms of haploid chromosome complements for five of the six species of the *Eleutherodactylus biporcatus* group. **A:** *E. gulosus*. **B:** *E. megacephalus*. **C:** *E. opimus*. **D:** *E. rugosus*. **E:** *E. biporcatus*—females and occasional males (2N = 36). **F:** *E. biporcatus*—most males (2N = 35), with the last three chromosomes being unpaired in diploid cells; the male heteromorphism was produced by a centric fusion between single chromosomes from pairs 17 and 18, with retention of the two other members as single chromosomes. See footnote 14. [Courtesy of Shyh-Hwang Chen.]

ficialis adductors are present (S + E condition). We do so because the presence of both a superfical adductor mandibulae muscle lying wholly laterally to the mandibular branch of the mandibular nerve (V_3), and a deeper muscle lying mesially to that nerve, seems to be a general pattern found in caecilians (Edgeworth, 1935; Bemis et al., 1983) and most (nonpaedomorphic) salamanders (Luther, 1914; Francis, 1934; Edgeworth, 1935; Baird, 1951; Carroll and Holmes, 1980), as well as in some groups of anurans. This pattern (S + E) therefore appears primitive for tetrapods.

We agree with Lynch (1986) that although the E condition has originated independently in several different anuran families, it may be regarded as a synapomorphy for the Middle American clade (subgenus *Craugaster*) within the Leptodactylidae. If our interpretation of jaw muscle evolution is correct, the S condition cannot be considered plesiomorphic to the E character state but has an independent origin from an ancestral S + E condition. This in turn suggests a relatively ancient separation of two major lineages within *Eleutherodactylus* s.l.

Although the condition of the adductor muscle clearly aligns the Venezuelan *Eleutherodactylus biporcatus* s.s. with the Middle American clade, its karyotype (unfortunately uncorroborated, see footnote 14) and different morphology (coarsely areolate venter, inner tarsal fold, accessory palmar and plantar tubercles, and male vocal slits) cast doubt on its putative relationship to the Central American species of the "*biporcatus* group" as treated in the present paper. Unsatisfying as it is, we must leave final solution of this remaining puzzle to future workers.

ACKNOWLEDGMENTS

We are immensely grateful to Dr. Rainer Günther for lending the type material of *Hylodes rugosus* and *Strabomantis biporcatus* from the Zoologisches Museum in Berlin (ZMB)—the present paper could not have been written without access to these critical specimens.

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APPENDIX: SPECIMENS EXAMINED

Collection Abbreviations: The following abbreviations of institutional collections are used in the text and in the list of specimens examined:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CRE,	Costa Rican Expeditions (collection now at Los Angeles County Museum of Natural History)
FMNH	Field Museum of Natural History
KU	Museum of Natural History, University of Kansas
MCZ	Museum of Comparative Zoology, Harvard
SMF	Natur-Museum und Forschungs-Institut Senckenberg
UCR	Universidad de Costa Rica, Museo de Zoología
UMMZ	University of Michigan Museum of Zoology

USNM	National Museum of Natural History, Smithsonian Institution
UTA	University of Texas at Arlington
ZMB	Zoologisches Museum an der Humboldt-Universität zu Berlin

Note: Some 40 specimens indicated by "***?**" after a KU number are assigned to *E. megacephalus* or *E. opimus* on the basis of geographic probability (see page 33), although specimens from one locality (Río Changena, B. del T.) conceivably might instead represent *E. gulosus*. Mostly collected by Myers, and by Duellman and Myers, these specimens were lost or misplaced in the University of Kansas collection before we could confirm identifications.

Eleutherodactylus aphanus

Guatemala: *Izabal:* 12.0 km WSW Puerto Santo Tomás, 786 m, UTA A-33405 (ad. ♂ holotype); also the paratypic series designated in original description.

Eleutherodactylus biporcatus (*E. maussi* auctorum)

Venezuela: *Aragua:* Rancho Grande [= 910–1170 m], AMNH 70533–70552, 70554–70558, KU 166369–166371, 166373–166374, 185671. *Miranda:* Guatopo, KU 185672.

Eleutherodactylus gulosus

Costa Rica: *Limon:* "Spur of the Pico Blanco" [= Cerro Utyum], 6,000 ft., USNM 32590 (ad. ♀ holotype, *Lithodytes gulosus*). **Panama:** *Bocas del Toro:* Gutiérrez, MCZ 9910–9914 (juvs). Río Claro near junction with Río Changena, 910 m, KU 115221 (juv.). *Chiriquí:* upper Río Chiriquí, Fortuna Dam Site, 1000 m, AMNH 95035–95046 (juvs.). South slope Quebrada de Arena, 1120 m (upper Río Chiriquí drainage, 82°12′43″W, 8°46′32″N), AMNH 114676, 124372, CRE 10365–10366. Continental divide above upper Quebrada de Arena, 1160–1220 m (at longitude 82°13′W), AMNH 124365–124369 (juvs.), 124370, 124371. 12.6 km N Los Planes on Gualaca–Chiriquí Grande Road at continental divide, 1180 m, USNM 339792 (juv.).

Eleutherodactylus megacephalus

Costa Rica: No other data, KU 34991 (11 juv.). *Alajuela:* Boca Tapada, UCR 12595. 4 km S Canelete, UCR 6746. Nr. Cariblanco, 853 m, CRE 6424. Colonia Libertad, UCR 10529. 4.8 km SW El Tanque, 80 m, CRE 7154 (8). 3 km W La Fortuna, 350 m, CRE 8078. 4 km W La Fortuna, 396 m, CRE 7152 (2). La Palma, nr. Dos Rios, UCR 10185. Pitilla Biol. Station, 600–825 m, CRE 10435. 8 km W Quesada, 250 m, CRE 7156 (2). Reserva San Ramón, UCR 10019–10026, 11171, 11417, 11448, 11450, 11453, 11456. Tabacón, UCR 3794–3795. *Cartago:* El Silencio de Sitio Mata, 1200 m, CRE 232, 235 (6), 237. Morehouse Finca, KU 53546. Turrialba, KU 28176–28182, 30771, 34992. *Guanacaste:* between Cañas and Tilarán, KU 53595. San Bosco, 700 m, CRE 6277 (2). El Silencio de Tilarán, 880 m, CRE 7066 (2). El Silencio de Tilarán, 910 m, CRE 6236. 3.5 km NNE Tilarán, 700–760 m, CRE 3698–3701. 5 km NE Tilarán, KU 36973–36977. Volcán Cacao, 1157 m, MVZ 207243–207244. Volcán Tenorio, UCR 10672. *Heredia:* E crest Barranca Río Sarapiquí, opposite Isla Bonita, 925 m, KU 65893. La Selva, 60 m, CRE 65, 67–69, 512, 699, 2970 (2), 3190 (3), 3385–3386, 3513, 3520–3521, 3523–3524, 3630, 4025, 4027, 6300, 6370, 6575, 8291, 8293, 8295–8296, 8361, 8339, 9701–9702, 9706, KU 157695–157700, 157704, UCR 705, 707. Puerto Viejo, KU 36952, UCR 363. 3 km E Puerto Viejo, 50 m, CRE 9731. 4 km E Puerto Viejo, UCR 316, 324. 4–6 km E Puerto Viejo, 50 m, CRE 3404–3406. 5 km E Puerto Viejo, UCR 3779–3780. Rara Avis, UCR 10611. Volcán Poas, KU 28174–28175. Zona Protectora La Selva, 320–400 m, CRE 7299, UCR 13275. *Limón:* 8–13 km SW Amubre, 300–500 m, CRE 7175. Bambú, 49 m, CRE 7183–7184. Cahuita, UCR 848. 8 km S Cahuita, UCR 381–382. Camadre, UCR 7903. Cerro Nimaso, UCR 8458, 8462–8463. El Tigre, 680 m, CRE 290 (3). Sendero a Gandoco de Manzanillo, UCR 9867–9869. 4 km W Guapiles, Río Toro Amarillo, 260 m, CRE 850. Katsi, UCR 3202. La Lola, 36–39 m, CRE 206–207, 500, 8068 (3), KU 34985–34990, UCR 3446. Los Diamantes, UCR 726. Pandora, 50 m, CRE 7191–7193. Penshurst, 4 m, CRE 3474. Reserva Biológica Hitoy-Cerre, UCR 11201, 11365. Río Toro Amarillo, 260 m, CRE 850 (2). About 18 km E. Siquirres, 300 m, AMNH 136244. Suretka, KU 36953–36955, UCR 3206. Tortugero N. P., Río Agua Fria Sta., 20 m (about 83°35′W, 8°27′N), CRE 8841–8844. **Honduras:** *El Paraiso:* Arenal, LACM 16847. **Nicaragua:** *Atlántico Norte (*formerly *Zelaya):* Backas Creek, AMNH 7268–7269. Cupitna Camp, AMNH 7270–7271, 7273–7274, 7300, 7302. Eden Mine, AMNH 7276–7281. *Atlántico Sur (*formerly *Zelaya):* Camp Corozo, Río Huahuashan, AMNH 54970. Camp Santa Ana, Río Huahuanshan, AMNH 54982–54984, 54996. Kanawa, AMNH 7267. Río Escondido, MCZ 15022, USNM 19909–19910. Río Patch, AMNH 55026. Río Pichinga, back of Pearl Lagoon, AMNH 55017–55018. *Matagalpa:* Jericó, BMNH 94.7.26.50. 19 km N Matagalpa, UMMZ 116453.

Río San Juan: Poderoso, AMNH 7293. Tuli [Tule] Creek [SE of San Miguelito], AMNH 7283, 7285–7286, 7289, 7291–7292, MCZ 7330–7331. **Panama:** *Bocas del Toro:* Almirante, MCZ 9893. Ca. 4.8 km W Almirante, 40 m, KU 108406***?.** Ca. 12.8 km W Almirante, 270 m, KU 108407–108410***?.** 10 km NW Almirante, FMNH 67713. 11 km NW Almirante, FMNH 67714–67716. 7.1 km airline WSW Chiriquí Grande, 70–100 m, AMNH 113983. Isla Bastimentos, ca. 0.8 km S mouth Alvarez (Alberry) Cr., USNM 297859. Isla Bocas del Toro [= I. Colón], FMNH 67712. Isla Colón, La Gruta, 20–80 m, KU 108411–108414***?.** Isla Colón, near La Gruta, AMNH 102239, USNM 338057–338067. Isla Colón, about 2.5 km N La Gruta, 40 m, AMNH 124395. East end Isla Escudo de Veraguas, 1 m, KU 113687–113689***?.** Isla Popa, 1 km SE Deer Island Channel, USNM 298035–298042. Isla Popa, 1 km E Sumwood Channel, USNM 347005–347009. Laguna de Tierra Oscura, 3.7 km S Tiger Key, USNM 348393–348394. La Loma (Buenavista), MCZ 9955–9961. Peninsula Valiente, Bluefields, 10 m, KU 108415–108424***?.** Peninsula Valiente, Punta Alegre, USNM 338604. Mouth of Río Cahuita, 1 m, KU 113690–113692***?.** Río Claro nr. junc. with Río Changena, KU 113682–113683***?.** Río Changena, 830 m, KU 108425–108429***?,** 113684–113686***?,** 115046***?.** Río Changuinola nr. Quebrada El Guabo (16 km airline W Almirante), 150–250 m, AMNH 107276–107282. Southwestern headwaters Río Guabo, 780 m (82°11′W, 8°47′N), AMNH 124392–124394. Southwestern headwaters Río Guabo, 530 m (82°11′30″W, 8°47′33″N), AMNH 124394. *Coclé:* Continental divide N El Copé, 600 m (longitude 80°36′W), AMNH 98367–98369. El Valle de Antón, ANSP 21750–21751, 23500, FMNH 67710. *Colón:* Gatún, ANSP 24855. *Panamá:* Barro Colorado Island, MCZ 15285–15287. Cerro Campana, FMNH 153694–153695. *Veraguas:* [Atlantic coast] mouth of Río Concepción, 1 m, KU 113676. [Pacific versant] 5–6 mi NW (via road) Santa Fe, AMNH 108344–108345.

Eleutherodactylus opimus

Colombia: *Chocó:* Quebrada Docordó, about 10 km above junction with Río San Juan, about 100 m, AMNH 87020 (subad. ♀ holotype). Quebrada Pangala, lower Río San Juan (about 17 km airline NE Palestina, nr. 4°15′N, 77°00′W), AMNH 109473–109487 (paratypes). Quebrada Taparal, lower Río San Juan (about 7 km airline NE Palestina, nr. 4°12′N, 77°07′W), AMNH 109471–109472 (paratypes). **Panama:** *Colón:* Río Boquerón, about 2.5 km (airline) N Peluca Hydrographic Station, 150 m, AMNH 89465 (paratype). "Río Chenillo" nr. Monte Lirio [probably Quebrada La Chinilla, inlet on Gatun Lake E of Monte Lirio, 9°14′N, 79°49′W], MCZ 11846 [tentative identification of juv. in poor condition]. Ridgetop trail SW Cerro Bruja, 240–370 m, KU 108430–108431 (paratypes). About 4 km SE Puerto Pilón, 190–240 m, KU 113677–113678 (paratypes). Río Guanche, 15 m, KU 172226–172228 (paratypes). *Darién:* Tarcarcuna, 550 m, KU 76221 (paratype). Laguna, 820 m, KU 76226 (paratype). Río Tuira at Río Mono, 130 m, KU 108934***?.**[15] *Panamá:* near community of Altos de Pacora (east of Cerro Jefe), 700–800 m, KU 108432–108433 (paratypes). 4.8 km N community of Altos de Pacora, on road to Mandinga, 740 m, KU 108434–108435 (paratypes). Candelaria and Peluca [hydrographic] stations, near Boquerón, AMNH 53704 (paratype). Cerro La Victoria, FMNH 67711. Cerro La Victoria, Quebrada Buenos Aires, FMNH 163863–163866. Km 11.7 on El Llano–Cartí Road, KU 172229***?.** Km 12.8 on El Llano–Cartí Road, 290 m, AMNH 89464 (paratype). East slope Cerro Jefe, 650 m, KU 80326 (paratype). Nusagandi, nr. Estación Ibe Igar, 350 m, CRE 10585, 10588. Nusagandi, about 2 km S Estación Ibe Igar, 300–350 m, CRE 10604–10605. Río Indio, trib. Río Chagres, USNM 102852. *San Blas:* Camp Summit, 300 m, KU 113679 (paratype), KU 113680–113681***?,** 113693–113694***?.**

Eleutherodactylus rugosus

No specific locality: "west coast of Central America", USNM 32326 (holotype, *Lithodytes pelviculus*). **Costa Rica:** *Puntarenas:* Aguabuena, KU 36978–36984. Quebrada Aguabuena, nr. Rincón de Osa, UCR 889–890, 909, 4575. 0.5 km NE Alfombra, 884 m, CRE 7097. Boruca, FMNH 3028. Río Carara, UCR 7723–7725. Cajón, UCR 7896. Cerro Puntado, 200 m, CRE 7139. El Helechales, 1050–1150 m, CRE 8268, 8272. Esquinas Forest Preserve, KU 34920–34922. Golfito, KU 34923. Las Cruces, 1100–1200 m, CRE 3182 (6 spec.), 3433, 3485, 3487–3488, 3889, 6583, 8435, 8618–8624, 8658–8662, 8667, 8691, UCR 1680, 6175–6176. Marenco Biol. Station, UCR 13878. Palmar, KU 34910–34919. 3.2–4.8 km W Palmar Norte, about 10 m, CRE 7101. 8 km NE Potrero Grande, 600 m, CRE 8279. 15–25 km E Potrero Grande, trail to 2nd savanna, 1000–1640 m, CRE 8276. Rincón de Osa, UCR 2651–2653,

[15] Based on color notes made by W. E. Duellman during his and Myers' 1965 Darién expedition into the upper Río Tuira region, the identification of KU 108934 as a member of the *biporcatus* group is open to question until the specimen can be found and reexamined.

UMMZ 123621. 2 km W Rincón de Osa, UCR 2066–2067, 4563, 4566. 3 km SW Rincón de Osa, 40–60 m, CRE 3506, 9202, 9249–9250. 3 km W Rincón de Osa, 25–300 m, CRE 3112, 9614–9619, 9639. 3 km WSW Rincón de Osa, 20–40 m, CRE 3429–3432, 9328. 3 km WSW Rincón de Osa, Camp Seattle, 20–30 m, CRE 705 (5 spec.), 752 (2), 754 (3). 3–5 km WSW Rincón de Osa, 20–30 m, CRE 3227. 5.5 km SW Rincón de Osa, 10–30 m, CRE 3495–3497, 7235, 9387–9388, 9665. 6 km SSW Rincón de Osa, 20 m, CRE 3148. Río Rincón, UCR 7607 12–15 mi WSW San Isidro de El General, KU 53567. San Pedrillo, UCR 11289. 2 km S San Vito, 1200 m, CRE 916 (2 spec.). Sirena, 5 m, UCR 11290–11291. Villa Neily, CRE 179. *San José:* Pozo Azul, BMNH 1907.6.28.24. San Isidro del General, KU 34908–34909. **Panama:** *Chiriquí:* No other data, ZMB 7812 (juv. holotype, *Hylodes rugosus*). Boquete trail, MCZ 11845. Progreso, UMMZ 58447–58449.

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